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## THE EFFECT OF THE MEDIUM ON APPARENT VITAMIN- SYNTHESIZING DEFICIENCIES OF MICROORGANISMS<sup>1</sup>

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Beadle and Tatum's work ('45) on biochemical mutants of *Neurospora* has resulted in wide acceptance of the view that it is relatively easy to distinguish strains genetically capable from those genetically incapable of synthesizing vitamins. They discovered many mutants apparently incapable of performing specific syntheses. The present paper reveals, however, that different synthetic media so affect the growth of organisms that conclusive demonstration of specific deficiency requires a much more critical study of the environment than has hitherto been achieved. Differential growth of cultures in a synthetic medium which deviates in many respects from the natural substrate may prove very useful for genetical diagnosis but may not give reliable information concerning the synthetic activity of the organism under normal conditions. Without critical testing it is difficult to say whether a given deficiency is absolute. The following data will show that the standard test of ability to grow in the presence and inability to grow in the absence of a given vitamin in a synthetic medium is inadequate and that the criterion of equal increments of growth for equal additions of the vitamin may give an ambiguous answer.

### A COMPARISON OF TWO SYNTHETIC MEDIA

Table I shows the formulas of the synthetic media used by Burkholder ('43), Hutner (unpublished), Wickerham ('46), and Beadle and Tatum ('45). Many experiments have shown that Hutner's medium is a very different substrate for yeast growth from Burkholder's. This was clearly revealed by growing cultures Nos. 3 and 10 (Table II) on two batches of each medium, one to which no pantothenate was added and the other containing 50  $\gamma$  of pantothenate per liter (fig. 1). Culture No. 3 does not begin to grow in Burkholder's medium without

<sup>1</sup>This work was supported by grants from Anheuser-Busch, Inc., The American Cancer Society, and Washington University.

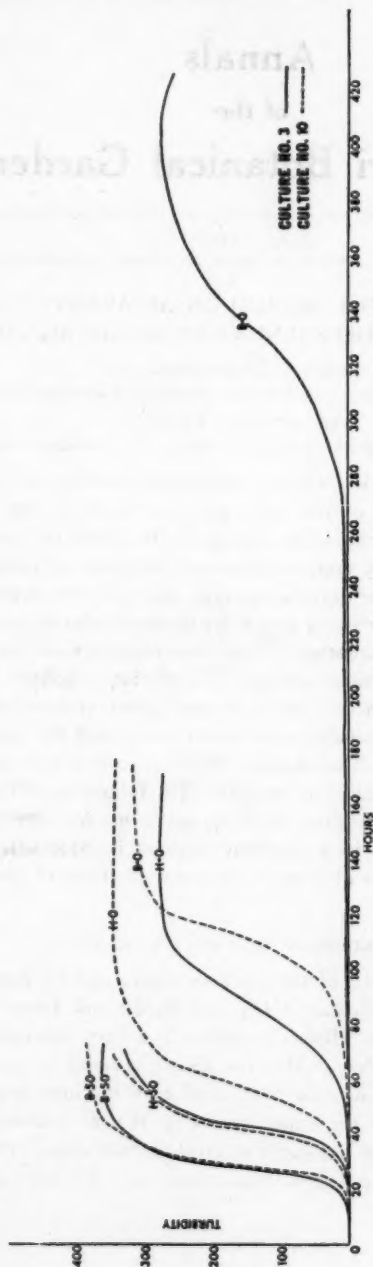


Fig. 1. Comparison of the amounts of growth on Burkholder's and Hutner's media. The turbidity indicated by a Klett Photoelectric Colorimeter is plotted against the time in hours after inoculation. Culture No. 3 was grown on two batches of Hutner's medium, one containing 50  $\gamma$  of pantothenate per liter and the other containing no added pantothenate. It was also grown on two different batches of Burkholder's medium, one containing 50  $\gamma$  per liter of pantothenate and one no added pantothenate. Culture No. 10 was also grown on these four different kinds of media.

added pantothenate until after 200 hours, but growth is completed in Burkholder's medium containing 50 $\gamma$  of pantothenate per liter after 50 hours. Readings taken at 72 hours would be interpreted to mean that it was a "nonsynthesizer." Culture No. 10 is capable of more rapid growth than culture No. 3 in Burkholder's without added pantothenate and it grows much more slowly in the absence of pantothenate than in its presence. Moreover, it synthesizes pantothenate after a considerable lag in Burkholder's medium; in Hutner's medium the lag is much shorter. Burkholder's medium is a much better diagnostic medium than Hutner's since growth occurs more rapidly on it than on Hutner's when pantothenate is supplied, but when pantothenate is not added, growth occurs less rapidly on Burkholder's than on Hutner's. That is, Burkholder's is a better medium when pantothenate is added but a poorer medium without added pantothenate.

#### THE "VITAMIN" PEDIGREE

Pedigree I (Table II) describes the melibiose-fermenting capacity of the various cultures which were subsequently investigated in some detail for their "vitamin-synthesizing" activity on Burkholder's medium according to his technique. The original diploid culture of *S. cerevisiae* (No. 1) was incapable of fermenting melibiose, and its offspring, cultures Nos. 3, 4, 5, and 6, were similarly incapable. In this pedigree numbers are used to indicate the different cultures, and each group of four in a single column includes the cultures produced by the four spores of a single ascus. Thus cultures 3, 4, 5, and 6 were originally from one diploid ascus of *S. cerevisiae*. Culture No. 2 (*S. carlsbergensis*) fermented melibiose, as did all of its haploid progeny. Culture No. 7 was the only survivor of a single ascus, and a mating between it and No. 4 produced a hybrid supposedly heterozygous for the ability to ferment melibiose.

This pedigree involves a non-Mendelian phenomenon which will be considered in greater detail in a later paper (Lindegren & Lindegren, '47). The pedigree is merely presented here for subsequent reference in tracing the descent of the different cultures.

#### HYBRIDS BETWEEN YEASTS SUPPOSEDLY DIFFERENT IN VITAMIN-SYNTHESIZING ABILITY

The members of this pedigree were characterized (Lindegren and Lindegren, '45) as "vitamin-synthesizers" and "vitamin-nonsynthesizers." The distinction between ability and inability to synthesize was made by Burkholder's method with his medium. This procedure defines readings taken at 72 hours as diagnostic. We have since discovered that this method does not give conclusive results, for if growth were allowed to continue, the supposedly nonsynthesizing yeasts will eventually begin to grow and will finally, in most cases, attain a level equal to that of the so-called synthesizers. However, at the end of 72 hours a 10- or 20-fold difference in growth often exists as indicated by reading the turbidity with a Klett Photoelectric Colorimeter. Haploids of *S. carlsbergensis* were characterized

TABLE I  
FORMULAS OF DIFFERENT SYNTHETIC MEDIA

	Burkholder's	Hutner's	Beadle & Tatum's	Wickerham's
	Grams per liter			
Dextrose	20.0	20.0		10.0
Sucrose			20.0	
Recrystallized asparagine	2.0			1.0*
K <sub>2</sub> HPO <sub>4</sub>				0.125
KH <sub>2</sub> PO <sub>4</sub>	1.5	1.0	1.0	0.875
MgSO <sub>4</sub> ·7H <sub>2</sub> O	0.5	0.2	0.5	0.5
CaCl <sub>2</sub> ·2H <sub>2</sub> O	0.33	0.037	0.1	0.1
(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub>	2.0			1.0*
KI	0.0001			0.0001
NaCl			0.1	0.1
Sodium citrate		0.8		
Citric acid		0.2		
(NH <sub>4</sub> ) <sub>2</sub> HPO <sub>4</sub>		0.8		
Ammonium tartrate			5.0	
(NH <sub>4</sub> )NO <sub>3</sub>			1.0	
	Parts per million			
Boron	0.01		0.01	0.01
Manganese	0.01	0.5	0.02	
Zinc	0.07	4.0	2.00	0.07
Copper	0.01	0.1	0.10	0.01
Molybdenum	0.01		0.02	
Iron	0.05	4.0	0.20	0.05
	Micrograms per liter			
Thiamin	200	200		400
Pyridoxine	200	200		400
Nicotinic acid	200	200		400
Pantothenate	200	200		400
Biotin	2	2	5.0	2
Inositol	10,000	10,000		2,000
Riboflavin				200
p-amino-benzoic acid				200
	pH 5.0 with NaOH	pH 6.0 with citric acid		pH 5.3

\* Either asparagine or (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> was used.

as biotin +, pantothenate +, and pyridoxine —; haploids of *S. cerevisiae* were characterized as biotin —, pantothenate —, and pyridoxine +, according to Burkholder's technique.

Table III shows the Klett readings obtained after 72 hours by Burkholder's technique of these different cultures. It appears that culture No. 4 is a non-synthesizer of pantothenate, while No. 7 is a synthesizer. A hybrid between No. 4

TABLE II

PEDIGREE OF A HYBRID BETWEEN *S. CEREVISIAE* (LK) AND *S. CARLSBERGENSIS* (MRAK, 126)

1	<i>S. cerevisiae</i> me diploid (Lk)			2	<i>S. carlsbergensis</i> Me diploid (Mrak, 126)			
3	a	me		7	a	Me	74 Me	
4	a	me		76		Me	80 Me	
5	a	me		77		Me	81 Me	
6	a	me		78		Me	82 Me	
				79		Me	83 Me	
<hr/>								
4 × 7 (a me × a Me)								
<hr/>								
10 diploid								
20	a	Me	12 Me	16 Me	35 Me	90 Me	94 Me	110 Me
21	a	Me	13 Me	17 Me	36 Me	91 me	95 Me	111 Me
22	a	Me	14 Me	18 Me	37 me	92 Me	96 Me	112 Me
23	a	Me	15 Me	19 Me	38 Me	93 Me		
<hr/>								
4 × 20 (a me × a Me)								
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	25 Me	29 Me	33 Me	39 me				
	26 Me	30 me	34 me	40				
	27 me	31 Me	35 Me	41 Me				
	28 me	32	36 me	42 me				
<hr/>								
5 × 23 (a me × a Me)								
<hr/>								
45 Me	49 Me	53 me	57 Me	61	65	69 me	86 Me	
46	50 me	54 me	58 me	62	66 me	70 Me	87 Me	
47 me	51	55 Me	59 Me	63 me	67	71 Me	88 me	
48 me	52	56	60 me	64 Me	68 Me	72 me	89 me	
<hr/>								
20 × 23 (a Me × a Me)								
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124 Me	128 Me	136 Me	140 Me	144 Me	150			
125 me	129 Me	137 Me	141 me	145 Me	151 Me			
126 me	130 Me	138 Me	142 Me	146 Me	152 Me			
127	131 Me	139 Me	143 Me		153 Me			
<hr/>								
4 × 49 (a me × a Me)				4 × 55 (a me × a Me)				
<hr/>				<hr/>				
	104 Me			117 me	121			
	105 me			118 Me	122			
	106 me			119	123			
				120 Me				
<hr/>								
5 × 72 (a me × a me)				7 × 72 (a Me × a me)				
<hr/>				<hr/>				
98 me	101 me			Me	me			
99 me	102 me			Me	Me			
100 me	103 me			Me	Me			
				Me				

and No. 7 (culture No. 10) appears capable of synthesizing pantothenate, but the four haploid progeny, Nos. 20, 21, 22, 23, do not reveal any segregation for this character according to this specific criterion. (The pantothenate character does segregate according to Mendelian ratios in other pedigrees which do normally segregate regularly.) It was subsequently discovered that none of these cultures was a nonsynthesizer and that the data appearing in Table III do not give an adequate picture of the synthetic ability of the organisms. The inadequacy of this characterization will be dealt with in detail below.

#### VITAMIN-SYNTHESIZING ABILITY OF SUPPOSEDLY DEFICIENT YEASTS IN A NATURAL MEDIUM

Dr. F. W. Tanner, Jr. (unpublished) grew various members of pedigree I (Table II) in a natural medium containing molasses and corn-steep liquor for 72 hours. When the yeast and the medium were assayed it was found that under these conditions all the cultures synthesized similar amounts of the different vitamins. Apparently the cultures were not clearly differentiated by ability and inability to synthesize the vitamins, but were all capable of synthesis under favorable conditions.

#### CONTINUOUS OBSERVATION OF GROWTH

Our present technique, an example of which has been presented in fig. 1, requires a much longer observation period. Many of the same cultures were reinvestigated and were sometimes observed for as long as a month, readings being made over the entire period. This is quite different from the standard practice of discontinuing the experiment after 72 hours. If the period of observation was extended for a longer time, haploid cultures of *S. cerevisiae* (as well as of *S. carlsbergensis*) were found to be able to grow on Burkholder's medium in the absence of pantothenate. This was equally true of all the progeny of the hybrid, many of which had previously been described as "nonsynthesizers." In some cases there was a delay of more than 600 hours before growth began. We grew the cultures in 6 x 3/4-inch Kimble tubes and determined the amount of growth by measuring turbidity on the Klett Photoelectric Colorimeter adapted to take the larger tubes. This made it possible to make readings over the entire period without discarding them.

#### THE INADEQUACY OF THE CRITERION, EQUAL INCREMENTS OF GROWTH FOR EQUAL INCREMENTS OF VITAMIN

Culture No. 7 was planted in a series of media containing different concentrations of pantothenate, and the data produced a family of parallel curves (fig. 3 in following paper). If the experiment were terminated at an arbitrary time (standard practice in nearly all assay experiments), curves could be obtained in which equal increments of vitamin appear to produce equal increments of growth. The curves in fig. 2 were obtained by readings taken at various times. At 50 hours there appears to be a straight-line relation between the amount of added vitamin and

TABLE III  
THE AMOUNT OF GROWTH AFTER 72 HOURS OF CULTURES FROM PEDIGREE 1 ON  
BURKHOLDER'S MEDIUM DEFICIENT IN THE INDICATED VITAMINS

Culture No.	Photometer Reading			Culture No.	Photometer Reading		
	—Py.	—Pa.	—Bi.		—Py.	—Pa.	—Bi.
1 (diploid)	350	220	11	4	350	15	12
2 (diploid)	24	280	280	5	310	20	8
				7	22	200	125

4 x 7

10 (diploid)	315	240	135				
20	274	45	50	12	355	293	170
21	312	202	55	13	80	65	160
22	290	200	59	14	350	220	75
23	300	210	110	15	25	15	7
90	318	212	140				
91	100	210	140				
92	300	235	134				
93	345	235	110				

4 x 20

25				33	340	12	10
26	310	25	145	34			
27	325	28	145	35	410	140	100
28				36	355	9	9

5 x 23

57	305	16	33	69	340	237	275
58	37	94	14	70	93	15	
59	38	100	10	71	358	16	230
60	347	16	20	72			
86	400	315	15	154	355	200	120
87	380	150	150	155	12	165	30
88	400	300	10	156	425	140	300
89	460	50	200	157	3	20	365

20 x 23

136	318	256	160				
137	360	222	193				
138	340	240	200				
139	320		170				

the amount of growth over a considerable portion of the curve. However, this culture was observed continuously, and eventually nearly as much growth was attained in the medium without the added vitamin as in the one containing relatively large amounts of added pantothenate (fig. 3 in following paper).

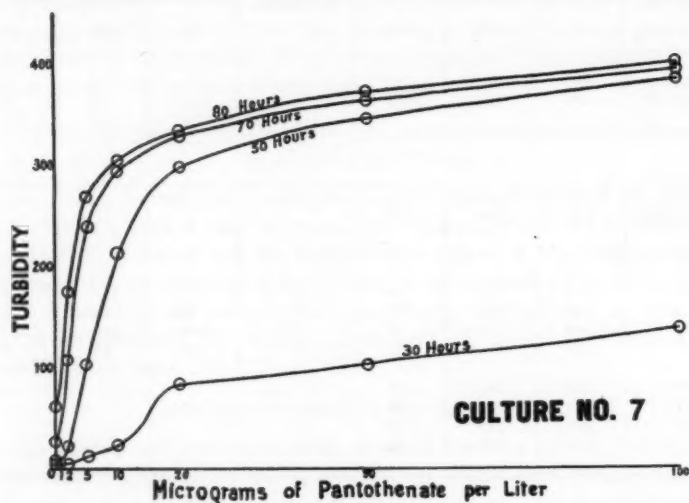


Fig. 2. The relationship between increments of pantothenate in Burkholder's medium and the amount of growth of culture No. 7 at different time intervals. In some phases of the curves a straight-line relationship exists between the amount of growth and the amount of added pantothenate but in all the culture tubes the growth eventually rose to approximately the same level.

#### THE EFFECT OF MULTIPLE DEFICIENCIES OF THE B VITAMINS

A haploid culture of *Saccharomyces cerevisiae* which grew well on an agar containing Hutner's synthetic medium with the vitamins, biotin, inositol, thiamin, and pantothenate, but which was unable to grow on the same agar medium lacking all these vitamins, was tested on agar containing various combinations of vitamins. Pour plates following Lederberg and Tatum's ('46) technique were made. In this technique a layer of sterile agar is poured in the bottom of the petri dish, then a layer of agar seeded with 500 cells poured on top, and a third layer of sterile agar on top of the second. This technique prevents colonies at the top and bottom of the agar from growing diffusely over or under the agar. A penicillin assay cup placed in the center of each plate was filled with a solution containing the combinations of vitamins.

Colonies were counted and a number of methods of scoring were tested, but simple + and - scoring is probably the most informative. The following tabulation gives the results:

VITAMINS PRESENT	VITAMINS ABSENT	SCORE
B I Th Pa		++ ++
I Th Pa	B	++ ++
B Th Pa	I	++ ++ ++
B I Pa	Th	++ ++
B I Th	Pa	++ ++
Th Pa	B I	++ ++
I Pa	B Th	++ ++
I Th	B Pa	++ ++
B Pa	I Th	++
B Th	I Pa	—
B I	Th Pa	—
Pa	B I Th	++
Th	B I Pa	++
I	B Th Pa	++ ++
B	I Th Pa	—
	B I Th Pa	—

The addition of inositol is apparently not very helpful in this concentration (10,000  $\gamma$  per liter) when biotin, thiamin, and pantothenate were also present, for there was more growth when it was absent than when it was present. Actually there were fewer colonies when it was absent, but those which grew did much better. However, the culture supplied pantothenate alone grew less well than that supplied both inositol and pantothenate. There were probably considerable amounts of biotin in the agar, for removal of biotin did not usually reduce growth greatly. Removal of biotin and inositol simultaneously was serious. When either inositol or pantothenate were removed singly no serious effect occurred, but when both were removed together there was considerably less growth. The cells could synthesize both inositol and pantothenate easily when only one was absent but lacking both they synthesized poorly. These facts indicate that inability to grow in the absence of vitamins may involve simply lack of capacity to grow, or begin to grow, under the prescribed conditions rather than inability to synthesize the absent vitamins under all conditions (Williams, '41).

#### THE RELATION BETWEEN VIABILITY OF CELLS AND INABILITY TO GROW ON DEFICIENT MEDIUM

The ability or inability to grow in a deficient medium may merely involve inviability in the new medium rather than absolute inability to synthesize the vitamin in question. If the cells are inviable in the deficient medium they will be unable to begin synthesis of the required vitamin. The fact that most yeasts begin to synthesize when they are permitted to stand a sufficiently long time suggests that continued examination of cultures is necessary. This points up an important difference between *Neurospora* and yeasts. A conidium of *Neurospora* can put out a germ-tube and begin growth in distilled water, but if it is to continue growth

it must be immediately supplied with the substances which it requires. It is relatively difficult to establish a *dormant mycelium* capable of awaiting future developments. Probably one of the most important advantages of a single-celled form over a filamentous fungus is that the single-celled form can go through one or two divisions and settle down to dormancy while a filamentous organism with specialized spores must continue to grow once the filament is produced or it will perish. This may give the appearance of absolute deficiencies to many mutants which die shortly after producing a filament in a medium lacking a specific vitamin.

These results have been supported by further work on three other mutants differentiated by ability to synthesize paraminobenzoic acid, pyridoxine, and uracil. So-called nonsynthesizers of pyridoxine eventually grew in a medium containing no added pyridoxine. Diploids heterozygous for a gene controlling synthesis of paraminobenzoic acid produced two classes of offspring, one which grew rapidly and one which grew slowly in the absence of paraminobenzoic acid. Although these two classes were clearly differentiated, the weak synthesizers were always able to grow eventually. An even more important bit of confirmatory evidence was obtained from the stock incapable of synthesizing uracil. The uracil-deficient cultures responded quickly to large amounts of uracil added to Burkholder's medium, but in the medium without added uracil they died. Transfer from uracil-deficient medium to a complete medium a few days after inoculation proved that the cells had died.

#### CONCLUSIONS

(1) Our results indicate that all so-called "nonsynthesizing" yeasts which remain alive when incubated in a deficient medium will eventually grow and synthesize vitamins in that medium.

(2) We have decided that Burkholder's conclusion that certain yeasts are "nonsynthesizers" requires qualification because synthesis might have been discovered if observation were made over a longer period.

(3) We suggest that many of Beadle and Tatum's "vitaminless" mutants may appear to be "nonsynthesizers" because they die in the deficient medium. "Reversions" of *Neurospora* mutants to wild-type, i. e., slow growth of "vitaminless" mutants in the deficient medium have been reported by Bonner, Tatum, and Beadle ('43) and other workers in this field, but they are usually regarded as exceptional cases rather than the standard expected behavior. The above results suggest the possibility that an improvement of the medium, without addition of the vitamin for which the stock is deficient, might lead to a higher frequency of reversions.

# A DIRECT RELATIONSHIP BETWEEN PANTOTHENATE CONCENTRATION AND THE TIME REQUIRED TO INDUCE THE PRODUCTION OF PANTOTHENATE-SYNTHESIZING "MUTANTS" IN YEAST<sup>1</sup>

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This paper describes experiments indicating that the concentration of pantothenate bears a direct relation to the time required to restore pantothenate synthesis in a yeast cell. Various members of the pedigree shown in Table II<sup>2</sup> were grown in batches of Burkholder's medium made up with the following amounts of pantothenate added per liter: 100, 50, 20, 10, 5, 2, 1, 0.5, and 0  $\gamma$ . Each tube was inoculated in a uniform manner with a loop. Three hundred colonies grew from each loopful of cells on plating, but since the haploid cells were typically aggregated the total number of cells was probably less than 1500.

Figure 3 shows the results with *S. cerevisiae* (culture No. 1), the turbidity being plotted against time in hours. The graphs are made by plotting the average of the turbidity produced in duplicate tubes, except in a few cases in which the tubes were so widely different that averaging did not seem to be a permissible practice. Usually the readings differed by only a few units and averaging was obviously acceptable. After 45 hours, growth is practically completed in the media containing 50 and 100  $\gamma$  of pantothenate, but it is fully 75 hours before appreciable growth is recorded in the tube without the added pantothenate. This culture had previously been characterized as a synthesizer of pantothenate. These data show that diagnosis depends largely on the time at which readings are taken. Comparison of the 100  $\gamma$  and 0  $\gamma$  tubes at the end of 45 hours would have resulted in characterizing this particular organism as a "nonsynthesizer" of pantothenate. The relationship between the amount of added pantothenate and the time at which growth begins is quite clear, since the curves are all closely parallel during early and logarithmic growth and overlapping occurs only after the logarithmic phase of growth has been completed. There is a sharp difference between the time at which growth begins in the tubes containing 0.5 and 1  $\gamma$  of pantothenate per liter as well as between growth in tubes containing 1 and 2  $\gamma$  of pantothenate per liter.

The culture of *S. cerevisiae*, whose reactions are recorded in fig. 3, was induced to sporulate, and similar tests with the four haplophase cultures are shown in figs. 4 and 5. Cultures No. 3 and No. 4 are remarkably similar in behavior. According to previous techniques, these would have been classified as "nonsynthesizers" because growth in the absence of pantothenate did not begin until after 250 hours. The particularly interesting feature of the behavior of these cultures is the direct relation between the length of the delay before growth begins and concentration of pantothenate in the medium.

<sup>1</sup>This work was supported by grants from Anheuser-Busch, Inc., The American Cancer Society, and Washington University.

<sup>2</sup>See preceding paper.

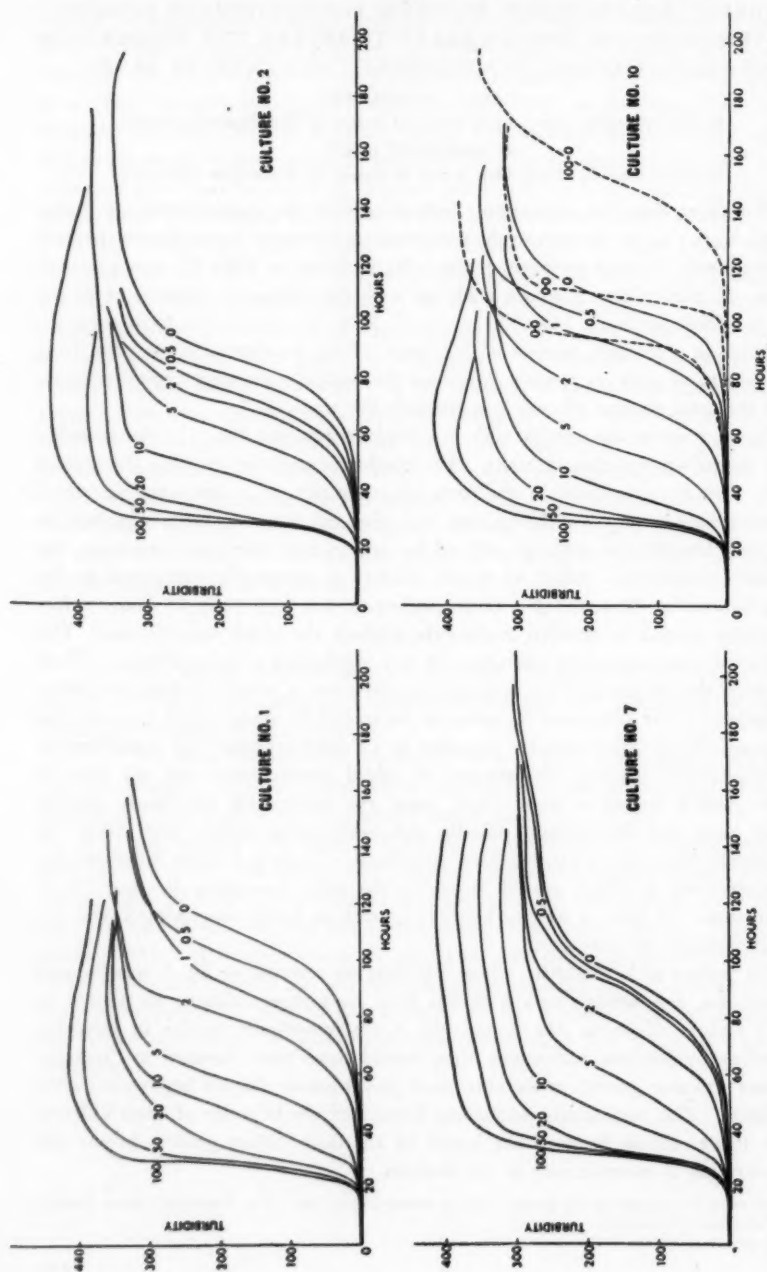


Fig. 3. The growth of cultures Nos. 1, 2, 7, and 10 in Burkholder's medium containing different concentrations of pantothenate. The solid lines represent the original inoculations; the dotted lines represent transfers from these inoculations as indicated, 100-0 being a transfer from 100 to 0.

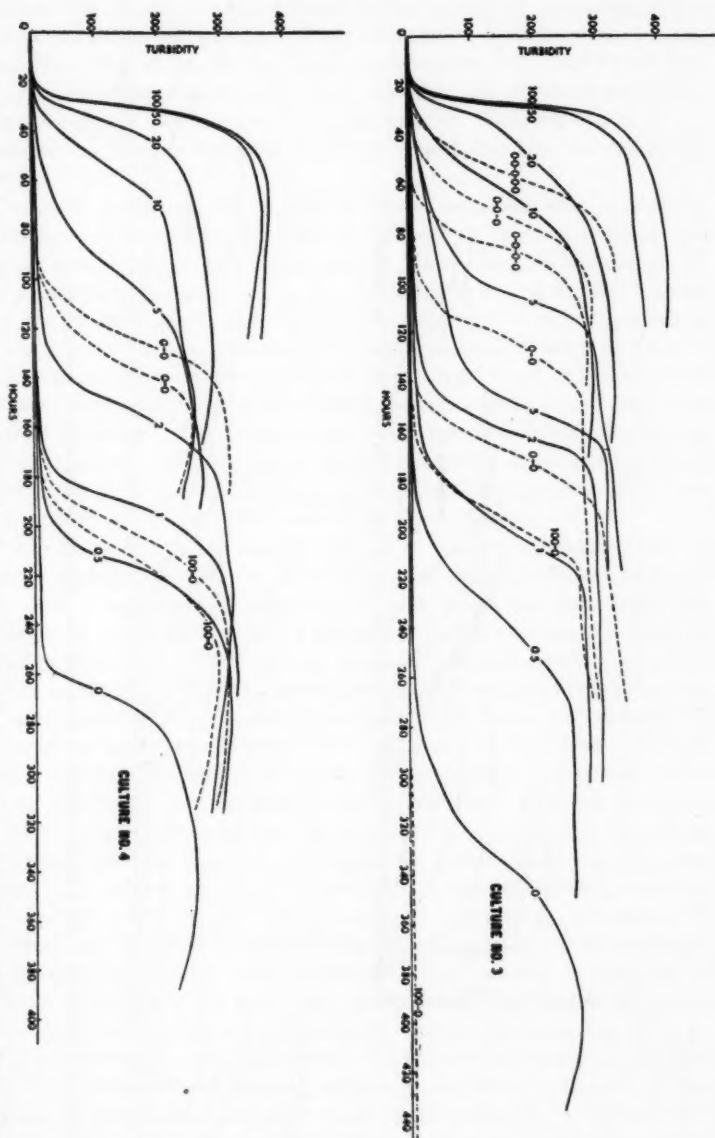


Fig. 4. Growth of cultures Nos. 3 and 4 on Burkholder's medium containing different concentrations of pantothenate. (The solid lines represent the original inoculations; the dotted lines represent transfers from these inoculations as indicated, 100-0 being a transfer from 100 to 0.).

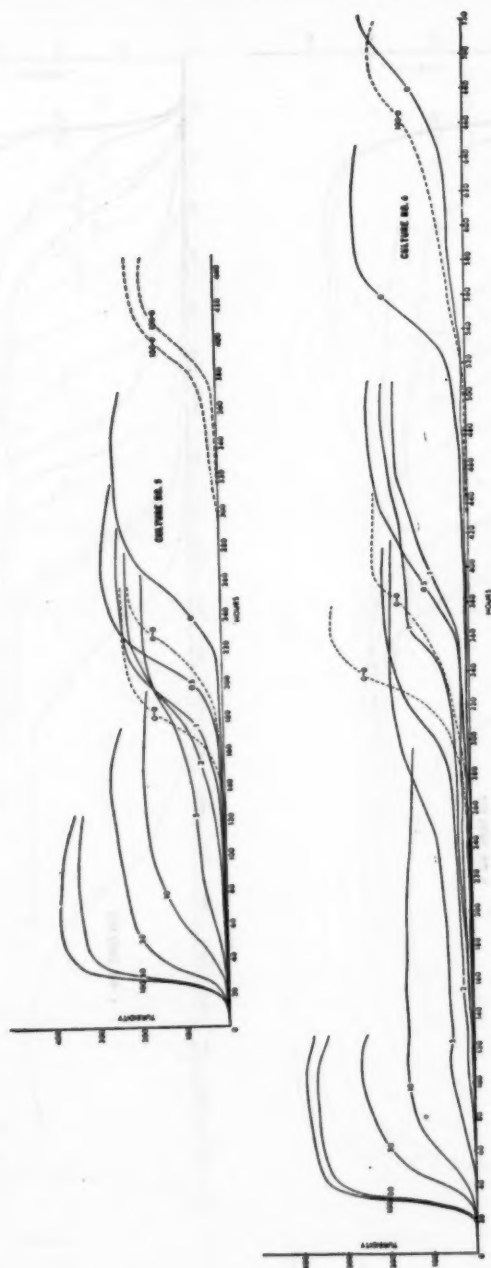


Fig. 5. Growth of cultures Nos. 5 and 6 on Burkholder's medium containing different concentrations of pantothenate.

In culture No. 5 (fig. 5) the different concentrations of pantothenate also bear a direct relation to the delay before growth begins. A similar picture exists for culture No. 6 (fig. 5), except that in the concentration of 1  $\gamma$  and 0  $\gamma$  per liter the duplicate tubes differed so markedly from each other that it was not permissible to average the results. This is one of the few cases in which growth in 1  $\gamma$  per liter in one of the duplicate tubes occurred later than that in the tube containing 0.5  $\gamma$  per liter.

The behavior in culture No. 5 (fig. 5) shows an almost ideal example of general tendency of the "delayed" cultures. Growth in media containing 100 and 50  $\gamma$  per liter takes place at a very rapid rate. In the medium containing 20  $\gamma$  the rate is somewhat decreased, and in 10  $\gamma$  considerably so. A further decrease occurs in 5  $\gamma$  per liter, so that there is a continual decrease in rate of growth in the 50, 20, 10 and 5  $\gamma$  media, respectively. The case is quite different in the 2, 1, 0.5 and 0  $\gamma$  media, where beginning of growth is delayed more and more as the concentration decreases but once growth begins the rate is uniform and more rapid than in the 5  $\gamma$  medium. The decreasing rate in the first five curves indicates that where there is an excess of pantothenate the growth bears a direct relation to the concentration of pantothenate, indicating that synthesis is suppressed when more than 5  $\gamma$  per liter are present. (See also culture No. 4, fig. 4).

The rate of growth in the last four curves is practically identical, but the delay before growth begins bears a direct relation to the concentration of pantothenate. This is interpreted to mean that in each of the last four curves the growth begins after the induction of a "mutation" which possesses the ability to synthesize pantothenate and that the rate of growth depends on the synthesis of the vitamin by the cell. The basic assumption for this interpretation is the view that *de novo* mutations from inability to ability to synthesize are extremely infrequent and the mutations observed in the laboratory are practically all "loss" mutations. On this assumption, an agent which produces regular and precise changes in cells from "nonsynthesizers" to "synthesizers" does not produce a change of a completely non-existent locus to a synthesizing locus but merely acts to bring a partially degraded or temporarily inactive gene into functional activity. The rate of growth is independent of the concentration of pantothenate originally present in the medium (below 2  $\gamma$  per liter). However, the time at which the "mutation" is induced (the "delay") depends on the concentration of pantothenate present; possibly directly on the number of molecules of pantothenate impinging on the gene. In a medium containing 1  $\gamma$  per liter, more molecules would collide with any given surface than in one containing 0.5  $\gamma$  per liter. The fact that only a small number of cells was used in inoculating the tubes and that easily detectable and constant differences exist between the low concentrations indicate that mutation occurs in many of the viable cells in a given tube at approximately the same time, rather than that one cell mutates and then outgrows its neighbors. If the latter were the case, the curves would overlap and the precise differences between the different concentrations would not be detectable. It

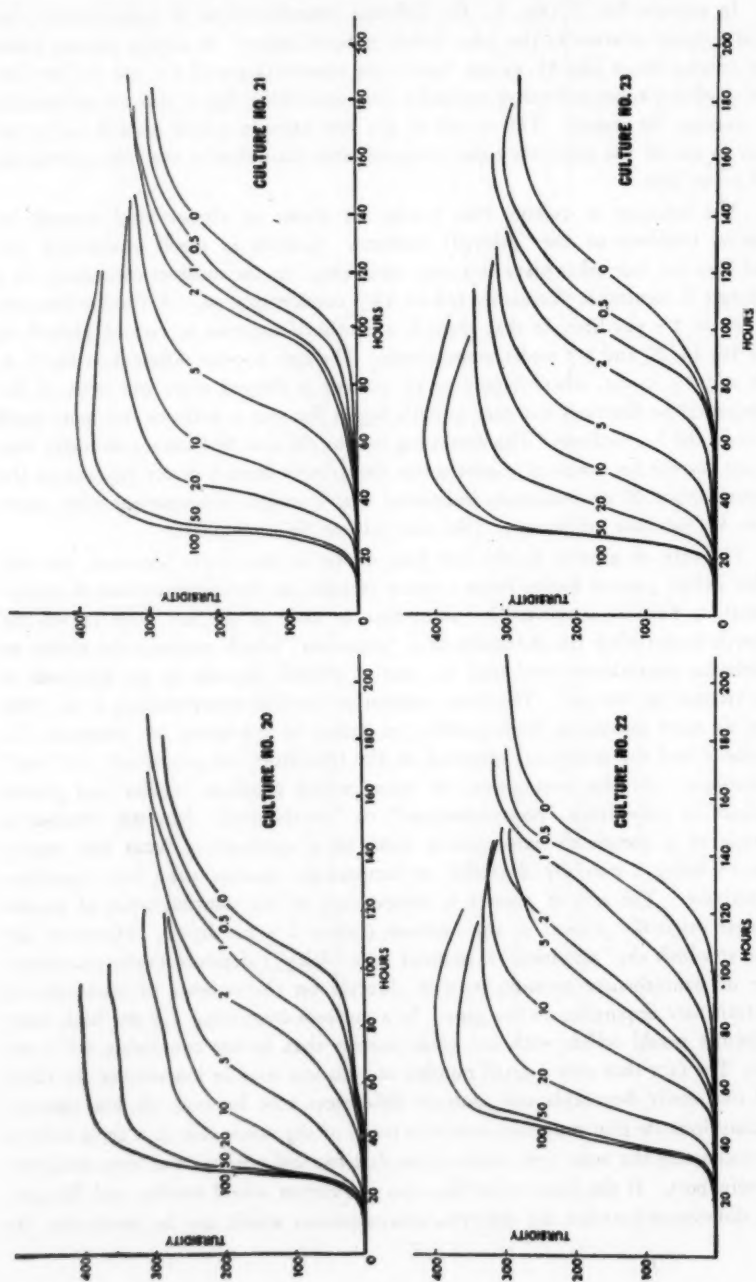


Fig. 6. Growth of cultures Nos. 20, 21, 22, and 23 on Burkholder's medium containing different concentrations of pantothenate.

is, of course, difficult to call these organisms "mutants" because the specific test for mutation is segregation. When transfers from the culture tubes without the added pantothenate were made to similar tubes likewise without added pantothenate (0-0) growth occurred about 150 hours sooner in the second than in the original test. These curves of growth are shown as dotted lines on the graph. As the yeast was transferred serially in the 0 medium, the delay before growth started was further shortened. The fifth transfer (0-0-0-0-0) began to grow sooner in the medium without the addition of pantothenate than the cultures which had been originally classified as synthesizers.

The original cultures came from a slant of yeast extract agar. Cells were suspended in 10 cc. sterile distilled water, and transfers to Burkholder's medium were made with a loop of this diluted suspension to insure against transfer of vitamins. A small but uniform number of cells was transferred in each loop. Irrespective of the concentration of pantothenate in Burkholder's synthetic media none of these original transfers failed to grow, but each grew after the delay indicated on the graphs. Many other transfers were subsequently made from one tube of Burkholder's synthetic medium to another with the same concentration of pantothenate; all these resulted in growth. Generally speaking, 0-0 transfers began growth much sooner than the original transfer, indicating that a "mutation" had occurred in the first transfer and that growth began due to the "mutation" or that some new channel of synthesis was established which became more efficient with continued use.

*Saccharomyces carlsbergensis* (culture No. 2, fig. 3) is an undelayed synthesizer of pantothenate, and growth in all concentrations of pantothenate is completed before 100 hours. The single haploid offspring of *S. carlsbergensis* (No. 7, fig. 3) is similarly an undelayed synthesizer but is spectacularly capable of utilizing any available pantothenate, as is shown by the beautifully parallel curves on the different concentrations. A hybrid between undelayed synthesizer (culture No. 7) and delayed synthesizer (No. 5) produced the hybrid culture No. 10, which was an undelayed synthesizer (fig. 3). When four haploid progeny from hybrid No. 10, cultures Nos. 20, 21, 22, and 23 (fig. 6), were tested, all showed the ability to use whatever pantothenate was available, as evidenced by the parallel nature of the curves for different concentrations. However, these four progeny were all undelayed synthesizers of the vitamin, and no clear-cut Mendelian segregation occurred. This does not necessarily mean that the difference is not one under gene control, for this pedigree is one in which gene transformation frequently occurs. This matter is being dealt with in an article now in press (Lindgren and Lindgren, '47). The pantothenate character segregates regularly in other pedigrees in which Mendelian segregation of other gene-determined characters normally occurs.

#### DISCUSSION

*Non-Random "Mutation."*—Mutations are generally supposed to result from random changes in the gene which occur independently of substrate with a specific

frequency. The probability that spontaneous or induced mutations would produce adaptive or "progressive" changes in a gene are generally thought to be about as likely as that the act of throwing a wrench at a motor would result in an improvement in the machine. Skoog and Lindegren ('47) have presented evidence indicating that mutation to glucose utilization was influenced by the nature of the substrate. The above data suggest that "mutation" which enables the cell to synthesize pantothenate depends directly on the concentration of pantothenate in the environment. The "mutations" induced by pantothenate are quite different from the ordinary recessive mutations used in genetical Mendelian analysis; they may merely be the result of the addition to the gene of one of its essential components. Such a component might correspond to what I have called the *cytogene*.

This presupposes that pantothenate synthesis is under genetic control. Most previously described "vitaminless" mutants are probably genotypes unable to survive in the deficient synthetic medium. The genotypes which we described here synthesize pantothenate when the level of pantothenate in the medium drops below a certain minimum. However, it is suggested by the data that some pantothenate (either in the cell or in the medium) must be present before the synthesizing mechanism can operate.

*Organized versus Molecular Genes.*—The gene is probably a loosely organized complex structure rather than a precisely definable chemical compound. The tendency to conclude from (1) the experiments of Stanley (in which an isolated crystalline nucleoprotein was shown to produce the same effect as tobacco mosaic virus) and from (2) the experiments of Avery, McLeod, and McCarty (in which a nucleic acid was shown to be capable of transforming one type of pneumococcus into another) that the gene is either a crystalline nucleoprotein or a nucleic acid disregards the possibility that the nucleoprotein and the nucleic acid may be only a part of the organized structure making up the gene. The fact that thousands of molecules of the mosaic virus nucleoprotein are required to produce a single infection has been interpreted to result from the difficulty of securing infection with a single particle. An alternative interpretation is possible: it may be that only one particle in a thousand of the "purified" preparation is so organized that it is capable of infection. In the pneumococcus experiment the transformation may have been achieved because the complex which comprised the gene producing the smooth mutant form was brought into functional activity by the addition of a single nucleic acid, just as a machine can be made to operate by adding a single nut. This does not mean that the nucleic acid is the gene, any more than the nut is the machine. Our experiments with pantothenate show that by adding molecules of it to a suspension of yeast cells a cell incapable of synthesizing pantothenate could be transformed into one capable of performing the synthesis. The fact that a gene-controlling synthesis has become functional may not mean that a gene has been added but merely that one component of the complex which makes up the gene has been supplied. This component, though essential, may be only a part of the total organized structure.

## CONCLUSIONS

The evidence presented above indicates that in the presence of a large excess of pantothenate no synthesis of pantothenate occurs although growth of cells by utilization of the available pantothenate goes on at a very rapid rate. At concentrations not in excess of, but greater than the minimum required for growth, the cells do not synthesize, and the rate at which they grow is determined by the amount of pantothenate supplied. When the concentration of pantothenate is less than the minimum required for growth the cells "mutate" so that they are able to synthesize pantothenate and grow. The time required for this "mutation" to take place is determined by the small amounts of pantothenate which are present in the media. The data may not completely exclude the possibility that only a small fraction of the population has been affected and that selection has been an important factor in the phenomenon; further tests of this view are in progress. The present indications support the view that a large fraction of the population is involved and if this be true, pantothenate can be regarded as an agent which acts to repair a partially degraded gene. The data suggest that in the complete absence of pantothenate neither synthesis nor growth can begin. (The cells in the medium to which no pantothenate has been added did not necessarily begin growth in the absence of pantothenate, for each cell probably carried a sufficient amount to initiate growth.) Synthesis occurs in Burkholder's medium only if enough pantothenate to initiate synthesis but not enough to suppress it is present.

## ACKNOWLEDGMENTS

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## MENDELIAN INHERITANCE OF GENES AFFECTING VITAMIN-SYNTHESIZING ABILITY IN *SACCHAROMYCES*<sup>1</sup>

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Pedigrees describing both Mendelian and non-Mendelian inheritance of the ability to ferment carbohydrates in *Saccharomyces* have been reported by us (Lindegren and Lindegren, '47). Genes controlling the fermentation of galactose, maltose, or melibiose are transmitted in a regular Mendelian manner in some pedigrees, and in a non-Mendelian manner in others. Present indications are that this is due to the gene-to-gene transfer of some essential gene-component controlling fermentation. This phenomenon complicated the problem of genetical analysis of yeasts until regular Mendelian pedigrees were available.

The diagnosis of the fermentative ability of any selected culture is clear-cut, no difficulty being experienced in distinguishing a fermenter from a non-fermenter. In the present pedigree the fermentation of sugar is usually complete after 48 hours; the negatives do not ferment when held for three weeks. When regularly segregating pedigrees became available, the problem of genetical analysis of fermentative ability was capable of an uncomplicated solution.

Burkholder's medium (Lindegren and Raut, '47) is an excellent diagnostic medium for distinguishing pantothenate "synthesizers" from "nonsynthesizers," because a so-called nonsynthesizer grows rapidly in this medium containing pantothenate, but requires weeks or months to produce growth in its absence. However, genes affecting vitamin synthesis are apparently transmitted in some pedigrees in a non-Mendelian way similar to that displayed by genes controlling fermentation. The first pedigree on the inheritance of "vitamin-synthesizing" ability in *Saccharomyces* (Lindegren, '45) failed not only to reveal regular Mendelian inheritance of this ability but also of genes controlling the fermentation of carbohydrates. In our selected inbred strains, the ability to ferment galactose and maltose is transmitted in a regular Mendelian manner, and the present paper shows that genes affecting the synthesis of paraminobenzoic acid, pantothenate, pyridoxine, and thiamin are transmitted with corresponding regularity. These genes are described as "affecting" rather than "controlling" the synthesis of vitamins, because we have not discovered any absolute deficiencies in yeasts. Lindegren and Raut have shown that a so-called nonsynthesizer of pantothenate eventually will grow in a medium without the addition of pantothenate, although some cultures do not begin growth until they have stood in the tubes for nearly a month.

<sup>1</sup>This work was supported by grants from Anheuser-Busch, Inc., Washington University, and the American Cancer Society.

In genetical analysis, it is relatively unimportant whether absolute or partial deficiencies are dealt with; all that is required is a clear-cut differentiation of the haploid offspring of a hybrid into two different categories. This is easily effected in our present yeast pedigrees by using Burkholder's medium with and without added pantothenate. Genes affecting pantothenate and pyridoxine synthesis are easily diagnosed; the "nonsynthesizers" do not begin to grow until a week after planting while the "synthesizers" attain nearly full growth after 48 hours. The former may produce a turbidity reading of between 200 and 300, while the latter still show a reading of between 0 and 5. After the tubes have been held for two months it is difficult to distinguish them, but at 4 or 5 days the difference is pronounced. Cultures differing in genes which affect the synthesis of thiamin and paraminobenzoic acid show distinct differences at the end of 48 hours, but by the fourth day it is difficult to tell them apart. However, any clear-cut segregation of the progeny into two classes supplies the geneticist with an adequate gene "marker."

Table I describes 8 asci dissected from a hybrid heterozygous for mating type,

TABLE I  
ANALYSIS OF ASCI FROM A HYBRID HETEROZYGEOUS FOR MATING TYPE, FERMENTATION OF GALACTOSE AND MALTOSE, AND GENES AFFECTING THE SYNTHESIS OF PANTOTHENATE

(Ascospores from Hybrid 1426  $\times$  1428 (a G ma pan  $\times$  a g MA PAN) )

Culture No.	Type	G	MA	PAN	Culture No.	Type	G	MA	PAN
1					2				
2101	a	—	—	274	2105	a	+	—	5
2102	a	—	—	160	2106	a	—	+	190
2103	a	+	+	3	2107	a	—	+	2
2104	a	+	+	4	2108	a	+	—	254
3					4				
2109	a	—	+	6	2113	a	—	—	3
2110	a	+	—	2	2114	a	—	+	210
2111	a	—	—	145+	2115	a	+	—	220
2112	a	+	+	274	2116	a	+	+	0
5					6				
2121	a	—	+	0	2125	a	—	—	2
2122	a	+	—	200	2126	a	+	+	270
2123	a	+	—	5	2127	a	—	—	4
2124	a	—	+	345	2128	a	—	—	200
7					8				
2147	a	+	+	290	2151	a	—	+	4
2148	a	—	+	137+	2152	a	—	+	250
2149	a	—	—	3	2153	a	—	—	140+
2150	a	—	—	8	2154	a	—	—	4

galactose fermentation, maltose fermentation, and a pair of genes affecting the ability of the organism to grow in Burkholder's medium without added pantothenate. The — and + signs under the columns G and MA indicate whether or not the organism produced gas in a medium containing galactose or maltose respectively. The figures under the column PAN show the turbidity reading registered in a Klett Photoelectric Colorimeter, after four days in a culture tube of Burkholder's medium without added pantothenate.

TABLE II

ANALYSIS OF ASCI FROM A HYBRID HETEROZYGOUS FOR MATING TYPE, FERMENTATION OF GALACTOSE AND MALTOS, AND GENES AFFECTING THE SYNTHESIS OF PARAMINOBENZOIC ACID, THIAMIN AND PYRIDOXINE.

(Ascospores from Hybrid 2236 × 2090 (a G MA pab th py × α g ma PAB TH PY) )

Culture No.	Type	G	MA	PAB	TH	PY	Culture No.	Type	G	MA	PAB	TH	PY
1							4						
2409	α	+	—	—	—	+	2419	α	—	—	+	+	—
2410	α	—	—	+	+	—	2420	α	—	+	—	—	—
2411	α	+	+	—	—	+	2421	α	+	+	—	+	+
2412	α	—	+	+	+	—	2422	α	+	—	—	—	+
5							6						
2423	α	—	—	—	—	—	2427	α	+	—	+	+	—
2424	α	+	+	+	+	+	2428	α	—	+	—	—	—
2425	α	+	—	—	—	+	2429	α	—	—	—	+	—
2426	α	+	+	+	+	—	2430	α	+	+	+	—	+
7							8						
2431	α	+	+	—	+	—	2435	α	+	—	—	—	+
2432	α	+	—	+	+	+	2436	α	—	+	—	+	—
2433	α	—	+	+	—	+	2437	α	—	—	+	—	+
2434	α	—	—	—	—	—	2438	α	+	+	—	+	—
9							10						
2439	α	+	—	—	—	—	2443	α	+	+	+	—	—
2440	α	—	—	+	+	+	2444	α	—	+	—	—	+
2441	α	—	+	—	+	+	2445	α	+	—	+	+	—
2442	died						2446	died					
11							12						
2447	α	—	—	+	—	—	2451	α	—	—	+	—	+
2448	α	+	—	—	+	+	2452	α	—	+	—	+	+
2449	α	—	+	+	+	—	2453	α	+	+	—	+	—
2450	α	+	+	—	—	+	2454	α	—	—	—	—	—

TABLE II (Continued)

Culture No.	Type	G	MA	PAB	TH	PY	Culture No.	Type	G	MA	PAB	TH	PY
13							14						
2455	a	+	-	-	-	+	2459	a	+	+	-	-	-
2456	a	-	+	+	-	+	2460	a	+	-	-	-	+
2457	a	-	+	+	+	-	2461	a	-	-	+	+	+
2458	a	+	-	-	+	-	2462	a	-	+	+	+	-
15							16						
2463	a	+	+	-	-	+	2467	a	+	-	-	-	-
2464	a	-	+	+	+	-	2468	a	-	+	+	+	+
2465	a	-	-	+	+	-	2469	a	+	+	-	-	+
2466	a	+	-	-	-	+	2470	a	-	+	+	+	-
17							18						
2471	a	+	-	-	+	-	2474	a	-	+	-	-	-
2472	a	+	+	+	+	-	2475	a	+	+	+	+	+
2473	a	+	-	+	-	+	2476	a	+	+	-	-	+
19							20						
2477	a	+	+	+	+	-	2481	a	+	-	-	+	-
2478	a	-	-	-	+	+	2482	a	-	-	+	-	+
2479	a	+	+	+	-	+	2483	a	-	+	-	+	-
2480	a	-	-	-	-	+	2484	a	+	+	+	-	+
21							22						
2485	a	+	+	-	+	+	2489	a	+	+	+	+	-
2486	a	-	+	+	-	+	2490	a	-	-	-	+	+
2487	a	+	-	+	+	-	2491	a	+	+	-	-	-
2488	a	-	-	-	-	-	2492	a	+	-	+	-	+
23							24						
2493	a	+	-	-	+	-	2497	a	+	+	-	+	-
2494	a	-	-	-	+	+	2498	a	-	-	+	+	-
2495	a	+	+	+	+	-	2499	a	-	-	+	-	+
2496	a	-	+	+	-	+	2500	a	+	+	+	-	+
25							26						
2501	a	-	-	+	-	+	2505	a	+	-	+	-	+
2502	a	-	-	+	+	-	2506	a	-	-	+	+	-
2503	a	+	+	-	+	-	2507	a	+	+	+	+	+
2504	a	+	+	-	-	+	2508	a	-	+	-	+	-

Cultures 2111, 2148, and 2153 produced the recorded turbidity in the pantothenate-free medium after 48 hours and were discarded. They would doubtless have grown more, this being indicated by the + sign after the turbidity reading. Each ascus produced two cultures with a turbidity reading of less than 8 and two with more than 160 four days after inoculation. The genes controlling mating type, galactose fermentation, and maltose fermentation also segregated regularly in each of the eight asci.

Table II is a pedigree describing the cultures grown from the ascospores dissected from 24 asci. These asci are derived from a hybrid heterozygous for mating type, galactose fermentation, maltose fermentation, and genes affecting the synthesis of paraminobenzoic acid, thiamin, and pyridoxine. The + and — signs indicate whether or not the cultures ferment galactose or maltose, and whether they grow in Burkholder's vitamin-free medium. The readings on the paraminobenzoic- and thiamin-free media were made after 48 hours, while those in the pyridoxine-free medium were made after four days. Two of the cultures from each ascus produced heavy turbidity in the vitamin-free media while two produced practically no growth at the time diagnosis was made. The readings were all recorded numerically just as were the pantothenate readings shown in Table I, but for the purposes of clarity were converted into + and — signs in the table. The only exception to the expected Mendelian segregation of 2:2 in each ascus is found in asci Nos. 5 and 22 in which three fermenters of galactose were discovered, although the mating type, maltose fermentation, and vitamin characters segregated regularly.

Tests were made for linkage between all possible pairs of genes, and usually free assortment was indicated. In some cases linkage to each other or to different centromeres was suggested but the evidence was not sufficient to warrant definite conclusions. These data are presented to establish the fact that genes affecting vitamin synthesis may segregate in a regular Mendelian manner in selected inbred pedigrees.

#### ACKNOWLEDGMENT

We are indebted to Dr. E. L. Tatum for the information that one of the parent cultures was paraminobenzoic acid-deficient.

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From the Department of Medicine, University of Chicago, Chicago, Ill.  
The following is a report of the results of a study of the effect of  
the administration of a certain drug on the blood pressure of  
patients with hypertension. The study was conducted by the  
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## AMERICAN ORIGIN OF THE CULTIVATED CUCURBITS<sup>1</sup>

### I. EVIDENCE FROM THE HERBALS

### II. SURVEY OF OLD AND RECENT BOTANICAL EVIDENCE

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#### INTRODUCTION

There are four species of *Cucurbita* that rank as cultivated plants (*C. Pepo* L.; *C. moschata* Poir.; *C. maxima* Duch.; and *C. ficifolia*<sup>2</sup> Bouché), and there is good archeological evidence that the first three were present in the Americas in pre-Columbian times (see Carter, '45). However, it has never been decisively demonstrated that this group may not have been common to both Old and New Worlds as seems to have been the case with the white-flowered gourd, *Lagenaria sicerea* (Molina) Standl.

In the course of his investigation on the association of the cultivated cucurbits with the various Amerind cultures of the Southwest, the writer had occasion to examine most of the published work that concerns the origin of this group. The present report is an attempt to evaluate this evidence, and draw the indicated conclusions.

With the exception of *Cucurbita ficifolia*, the four species with which we are concerned are annuals. All have 20 pairs of chromosomes. They rarely, if ever, produce species hybrids, except by means of artificial pollination, and then only with difficulty. Up to the present, none have been discovered in the indigenous state.

### I. EVIDENCE FROM THE HERBALS

The herbals of the 16th and early part of the 17th centuries are invaluable sources of information in tracing the origins of the cultivated species of *Cucurbita*. Prior to the establishment of contact with the New World in 1492, the herbals contained no recognizable description or illustration of these plants. Surely plants as large and distinctive in vine and fruit as squash and pumpkins would not have escaped the notice of an astute group of observers such as the herbalist-scholars of the 15th century appeared to be. A century after the discovery of America, the record as traced through the various herbals indicates that two of the annual

<sup>1</sup>An investigation carried out while a Fellow of the John Simon Guggenheim Memorial Foundation, 1946-1947. The writer is grateful to the Director, Librarian, and staff of the Missouri Botanical Garden for their courtesy in making available for study the excellent collection of pre-Linnean literature found at that institution. Thanks are due to Professor Edgar Anderson for his customary stimulating advice and criticism.

<sup>2</sup>*Cucurbita ficifolia* is ordinarily not thought of as a cultivated plant. The work of the Russian investigators Bukasov, Zhiteneva ('30), Parodi ('34), and more recently the collections of Sauer, West, and others (personal communications), indicate that it has a long history of cultivation, and must be regarded as a cultigen. There are no archeological records of its occurrence. It is a perennial with 20 pairs of chromosomes.

species of *Cucurbita* had reached Europe, and one of them (*C. Pepo*) was represented by several varieties.

Fuchs (1542) seems to have been the first herbalist to note a cultivated cucurbit and produce a recognizable figure of it. His illustration, labelled "Türkisch Cucumer," is evidently some variety of *Cucurbita Pepo* (pl. 11, fig. 1). The deeply lobed leaves and general appearance of the plant suggest that it may be allied to our present-day Vegetable Marrows. From the shape of the fruit, there is reason to believe that the illustration labelled "Meer Cucumer" is a variety of *C. Pepo* currently known as "Small Sugar" (pl. 11, fig. 2). Like the illustrations of most herbalists, Fuchs' are somewhat conventionalized, in order to accommodate the plants to the size of the wood block, but there is no doubt that the figures mentioned are properly referable to *C. Pepo*.

Matthioli (1560) has an illustration of what seems to be a field pumpkin (*C. Pepo*) labelled *Cucurbita indica* (pl. 12, fig. 1). Daléchamps (1587) has a copy of this plate, which Seringe (1828) improperly assigns to *C. moschata*. Although the leaves are not as strongly dissected as typical *C. Pepo*, the pattern of the remaining morphological characteristics makes it seem certain that the plant is referable to this species.

Dodoens (1563) has produced a figure (*Pepones lati*) of what appears to be a form of *Cucurbita Pepo*. Judging from the shape of the fruit and the lack of tendrils, this form must be closely related to the present-day variety "White Bush Scallop" (pl. 12, fig. 2). Daléchamps (1587), in his *Historia generalis plantarum*, has illustrated, for the first time, a warted variety of *C. Pepo* under the name *Cucurbita verrucosa* (pl. 12, fig. 3). Bauhin (1650-51) has a reversed copy of Daléchamps' figure, and Bailey ('29) is undoubtedly correct in assigning it to *C. Pepo* even though the leaves and flowers do not conform very closely to this species.

Lobelius (1591) illustrates five varieties of *Cucurbita Pepo* (*Pepo oblongus*, *Pepo rotundus compressus* *Melonis effigie*, *Melo-pepones latiores Clypeiformes*, *Melo-pepo teres*, and *Melo-pepo compressus alter*). The fruits pictured under the label *Melo-pepones latiores Clypeiformes* are identifiable without doubt as a form of the scallop-fruited summer squash, probably the variety "Golden Custard" (pl. 12, fig. 4). Although definitely *C. Pepo*, the remainder are difficult to homologize with any of our present-day varieties. In addition, Lobelius has produced the first illustration of a plant definitely referable to *C. maxima*, under the name *Pepo maximus Indicus compressus* (pl. 12, fig. 5).

Tabernaemontanus (1591) is particularly rich in the number of varieties of *Cucurbita Pepo* which are illustrated. A total of nine forms are figured, some of which can be recognized as closely allied to our present-day varieties. *Melo-pepo clypeatus* is undoubtedly a form of the "White Bush Scallop" summer squash; *Cucurbita capitata* is much like the former with a slightly different fruit shape. *Melo-pepo teres* and *M. compressus* are apparently bush forms since they lack tendrils. The shape of the fruit indicates that *Pepo maximus oblongus* is probably a

Vegetable Marrow type; the same is true for *Pepo Indicus minor oblongus*. The form designated as *Pepo Indicus minor rotundus* is quite similar in shape to our modern variety, "Perfect Gem." *Pepo Indicus minor clypeatus* and *Pepo Indicus minor angulosus* (pl. 12, fig. 6) are forms whose fruit shape and general appearance are strongly reminiscent of the modern "Table Queen" or "Acorn" squash.

The results of this survey provide strong evidence that none of the cultivated species of *Cucurbita* were known to the botanists of the Western World before 1492<sup>3</sup>. In the following century at least two species (*C. Pepo* and *C. maxima*) were recognized by the herbalists, and for one of them (*C. Pepo*) a number of varieties were known. It seems strange that *C. moschata* was not introduced into Europe during this period. There may be several reasons for this: (1) In general, this species is more subject to range restrictions by low temperatures and short days than either *C. Pepo* or *C. maxima*; (2) recent distribution data indicate that it is found only in the more inaccessible regions of Mexico, Central America, and Colombia.

*Cucurbita ficifolia*, with its relatively hard shell and rather coarse, stringy flesh, lacks the edible qualities of the annual species. This may have been the chief reason for its neglect by the early explorers. Furthermore, this species requires a relatively long photoperiod, and it is doubtful whether it would mature fruits in Europe, except perhaps in the extreme southern portions and under exceptionally favorable cultural conditions.

## II. SURVEY OF OLD AND RECENT BOTANICAL EVIDENCE

### *Evidence for the Old World origin of the cultivated species of Cucurbita.*—

The concept that the cultivated species of *Cucurbita* were indigenous to the Old World appears to have originated with Naudin (1856). At the beginning of his extensive and illuminating memoir, which has laid the experimental foundation for our understanding of the species of this group, he devotes a single paragraph to their origin. He states that of the six known species (*C. moschata*, *C. Pepo*, *C. maxima*, *C. melanosperma*, *C. perennis*, and *C. digitata*) the first three have been cultivated for a considerable length of time in Europe. The nativity of *C. maxima* is admittedly undetermined. It is claimed, without documentation, that *C. Pepo* has been known to the Romans and Greeks at least since the time of Pliny. According to Naudin, *C. maxima* and *C. moschata* are more modern introductions into European gardens ("leur introduction dans nos jardins ne remontant guère au delà de deux siècles").

<sup>3</sup>Sturtevant ('19, p. 219) has summarized this line of evidence in a remarkable lucid statement, "If we consider the stability of types and the record of variations that appear in cultivated plants, and the additional fact that, so far as determined, the originals of the cultivated types have their prototypes in nature and are not the products of culture, it seems reasonable to suppose that the record of the appearance of types will throw light upon the country of their origin. From this standpoint, we may, hence, conclude that, as the present types have all been recorded in the Old World since the fifteenth century and were not recorded before the fourteenth, there must be a connection between the time of discovery of America and the time of appearance of pumpkin and squashes in Europe."

Naudin, in discussing *Cucurbita ficifolia* (*C. melanosperma* Gaspar.), states that it was introduced into Europe about 1800 A. D., probably from southern Asia as indicated from its common name, "Courge de Siam." Reports of travelers led him to believe that at this time it was grown in China on a large scale; thus confirming his opinion that the species originated in Asia. Naudin thought that *C. ficifolia* has important potentialities as an economic plant, for use as human food if properly prepared in the immature stages, and as cattle food because of its long-keeping qualities.

In a later paper, Naudin (1859) reports further experimental work with various genera of the Cucurbitaceae. He does not make any positive statement about the origin of the cultivated cucurbits, although he infers that *C. moschata* is an Old World indigene. He states that seed of several varieties collected in India have been grown at the Museum. Since the early terminology of cucurbitaceous fruits was in much confusion, it is highly probable that Naudin has mistaken Pliny's reference to watermelons, melons, cucumbers, and gourds as including some members of the genus *Cucurbita*. There is no evidence to support the belief that Pliny was familiar with the latter group.

The widely held conviction that the three commonly cultivated species of *Cucurbita* were of other than American origin was continued by De Candolle ('83) on very slender, and for the most part, questionable evidence. Later investigators (Cogniaux, 1881; Pittier, '26; Herrera, '41) have propagated De Candolle's views without critical reexamination of their basis. From De Candolle's discussion of the origin of the four species under consideration it is apparent that he is positively in favor of an Old World origin only in the case of *Cucurbita maxima*, and there is some reason to doubt that he felt that the record was entirely convincing here. In terminating his discussion of the origin of *C. maxima* he makes the statement, "En définitive, sans ajouter une foi implicite à l'indigénat sur les bords du Niger, fondé sur le dire d'un seul voyageur, je persiste à croire l'espece originaire de l'ancien monde et introduite en Amérique par les Européens."

The best evidence De Candolle could muster for his Old World theory of the origin of *Cucurbita maxima* was Hooker's (1871) citation of localities for certain collections: i. e. "Upper Guinea. Nupe on the Niger, apparently indigenous, Barter!" Welwitsch's discovery of this species in Angola is also referred to, but there is no indication as to whether or not it was an indigenous plant. The fact that Barter's plants were collected along the banks of a large river would lead to the supposition that it was an introduced species. Welwitsch's collection was made in or around a village, and it is therefore quite likely that the plants were escapes. At best, De Candolle's arguments for an Old World origin of *C. maxima* rest on an extremely flimsy foundation.

As for *Cucurbita Pepo*, De Candolle presents the documented evidence for and against its Old World origin. His position may be summed up by stating that the historical record does not contradict the opinion that this species may be of American origin.

According to De Candolle, the origin of *Cucurbita moschata* presents an unsolved problem. However, he is inclined to attach some weight to the unproven assertion that this species was more widespread in southern Asia than in any other region during the seventeenth century. As stated previously, *C. moschata* was unknown to the botanists of the fifteenth and sixteenth centuries. The first record of its occurrence seems to be the excellent illustration published by Van Rhede in *Hortus Malabaricus* (1688). During the 17th and 18th centuries it appeared in several floras of southern Asia and Africa (Wight, 1843; Clarke, 1879; etc.). However, in no case was it claimed to be an indigenous plant.

Evidently *Cucurbita moschata* was introduced into European horticulture from southern Asia (Naudin, 1856), rather than directly from the Americas. The common names given to varieties of this species were indicative of Old World origin, i. e. "Pleine de Naples," "Pleine de Barbarie," "Muscade de Provence," etc.

De Candolle suggests that *Cucurbita ficifolia* is of American origin, since up to the time of his investigations, all the perennial species of the genus were natives to California or Mexico, whereas the annual species were assumed to be of Old World origin. This argument has now lost whatever cogency it may have had. Bailey ('43) has described several species from North America which are undoubtedly annuals.

*Evidence for the New World origin of the cultivated species of Cucurbita.*—

In a critical review of certain phases of De Candolle's book, Gray and Trumbull ('83) present the evidence for an American origin of the three annual species. Their report can best be summarized by quoting directly:

"Allusion has already been made (under *Lagenaria*) to the difficulty of distinguishing the genera of the *Cucurbitaceae*, under names by which they are mentioned by voyagers and explorers of the first century after the discovery of America; and the question of species is particularly difficult. Yet we find abundant evidence—especially as respects North America—(1) that in various parts of the country, remote from each other, the cultivation of one or more species of *Cucurbita* by the Indians was established before those places are known to have been visited by Europeans; (2) that these species or varieties were novel to Europeans, and were regarded by botanists of the 16th and 17th centuries, as well as by the voyagers and first colonists, as natives or denizens of the region in which they were found; and (3) that they became known only under American names; one of these names (*Squash*) becoming, in popular use, generic, and two others (*Macock* and *Cushaw*) surviving, as names of varieties, into the present century."

Gray and Trumbull then present strong evidence for their conclusions, following a chronological scheme as nearly as possible. First, the reports of several early explorers and historians are cited. Although it is usually difficult or impossible to determine precisely to what species these writers have reference, it is almost certain that they are concerned with one of the three annual species of *Cucurbita*, probably *C. Pepo*. The reports of the following explorers are cited: Columbus, Cuba, 1492; Cabeça de Vaca, Florida, 1528; De Soto, Florida and Mississippi, 1539-41; Cartier, Canada, 1535; Sagard, Canada, 1642; Lahontan, Southern Canada, 1703; also the historians who mentioned pumpkins, macocks and squashes—Captain John Smith, 1606-08; Strachey, 1610; Higginson, 1629; Beverley, 1705; and others.

Further support is provided by the works of the 16th century herbalists—Fuchs, Dodoens, Matthioli, etc. It is clear, as Gray and Trumbull point out, that the Cucurbitas were considered foreign or novel by these botanists. Furthermore, the word "Indian" as applied to the area of origin of various species did not necessarily mean that they came from Asia, but rather the West Indies or the Americas. Much confusion has come about through a misinterpretation of the word "Indian." De Candolle and others have, for the most part, interpreted it in a narrow sense as applying only to British India, but the truth seems to be that *Cucurbita Pepo* and *C. maxima* reached Europe from the West Indies or directly from the American continent.

Gray and Trumbull regard Nuttall's (1818) statement of particular importance in establishing the American origin of the cultivated *Cucurbita*. Nuttall mentions two species, *C. Lagenaria* and *C. verrucosa* (Warted Squash), and of the latter, he observes, "Cultivated also by the Indians of the Missouri to its sources." *Cucurbita verrucosa* is one of the warted varieties of *C. Pepo*. Trumbull's work (1876) in tracing the Indian origin of the words squash, cushaw and macock is considered by Gray and Trumbull as being especially significant in establishing a case for the North American origin of *Cucurbita Pepo* and *C. moschata*. Trumbull states in summarizing his conclusions, "As regards North American varieties, the evidence seems conclusive. These varieties at least bear Indian names, which date from the first coming of the Europeans, and of these varieties we have no mention before they were found in North America."

*Recent botanical evidence.*—

The Russian plant explorers (Bukasov, '30; Zhitenewa, '30) have contributed an immense amount of data to our knowledge of the distribution of the cultivated Cucurbitas. Briefly, they have found that the greatest diversity of the group is found in Central Mexico, where *Cucurbita Pepo*, *C. moschata*, *C. mixta* (a variant of *C. moschata*), and *C. ficifolia* occur together under cultivation, in the same general area (Mesa Central). It is important to note the omission of *C. maxima* from the above list. Apparently this species has never been cultivated by the natives of Mexico, Central America, or the northern portions of South America.

*Cucurbita ficifolia*, according to the Russian investigators, is the most widely distributed species of the group. It is found in all countries from Mexico to Chile along the Cordillera. There are white-seeded and black-seeded forms; otherwise, the composition of the species is very stable over the entire range. *Cucurbita moschata* is almost as widely distributed as *C. ficifolia*. It is extensively grown in Mexico, Central America and Colombia, but does not extend southward to Peru and Chile. In Panama and Colombia it is the only cultivated species of *Cucurbita*. The forms found in Mexico and parts of Central America are typically white-seeded, while those of Panama and Colombia are brown-seeded. The Russians consider that the center of distribution of *C. Pepo* must lie to the north of the Mesa Central in Mexico, since it is completely absent from their South American collections, and appears only sparsely in their records from Central Mexico.

Parodi ('35) has made a significant contribution to the subject in his study of pre-Hispanic agriculture in Argentina. He finds that *Cucurbita maxima* was one of the principal species of plants cultivated by the Guaranes in northeast Argentina and Paraguay at the time of the conquest of the Rio de la Plata.

Cardenas ('44), after completing his studies of the cultivated Cucurbits of Bolivia, comes to the conclusion that there were several varieties of *Cucurbita maxima* present in the Andean valleys of South America at the time of the conquest. On the other hand, *C. Pepo* and *C. moschata* are evidently of recent introduction into the cultivated crop complex of Bolivia, Paraguay and Argentina. He suggests that a thorough exploration of the temperate and tropical portions of Bolivia and Peru might uncover wild relatives of the cultivated cucurbits that would be helpful in deciphering their relationships. The basis for this suggestion is the discovery of a small, warted gourd (el "joko") in an isolated region of Bolivia (upper canyon of the Rio Caine). This gourd is cultivated for food and is believed to be closely related to *C. Pepo*.

#### SUMMARY

1. Negative evidence of the presence of *Cucurbita Pepo* and *C. maxima* in Europe prior to 1492, also familiarity of the herbalists of the 16th and 17th centuries with these species, suggest very strongly that they were introduced into Europe from the Americas.

2. An examination of the evidence in favor of the origin of the cultivated species of *Cucurbita* in the Old World indicates that it is very fragmentary, and in general unacceptable.

3. The botanical record, while not as extensive or decisive as it might be, clearly favors an American origin of the cultivated cucurbits.

4. Finally, the archaeological and botanical records lead inescapably to the conclusion that the four cultivated species of *Cucurbita*, *C. Pepo*, *C. moschata*, *C. maxima*, and *C. ficifolia*, are New World in origin. The possibility that *C. moschata* may have been common to both hemispheres is not ruled out, but it does seem relatively remote.

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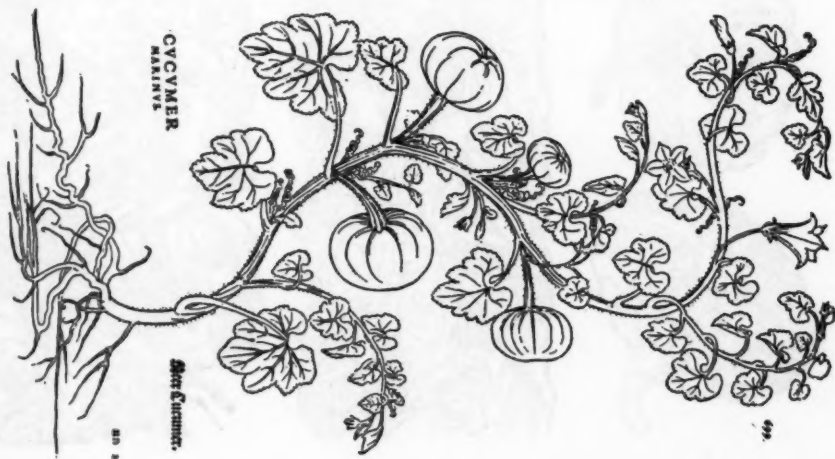
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## EXPLANATION OF PLATE

## PLATE 11

- Fig. 1. "Türkisch Cucumer" of Fuchs, apparently a variety of *Cucurbita Pepo*.  
 Fig. 2. "Meer Cucumer" of Fuchs, evidently *C. Pepo* var. "Small Sugar."



WHITAKER—ORIGIN OF CULTIVATED CUCURBITS

*CUCURBITA INDICA.*



1

*Pepoer lat.*

*Driede Pepoer.*



2

*CUCURBITA  
verrucosa L.*



3

*Melo-pepoer latioris Clypeiformes. T. 784.*



4

*Pepo maximus Indicus compressus. L. 363. T. 784.*



5

*Klein Ind'antisch edelsteig Pepoer.  
Pepo indicus minor angulosus.*

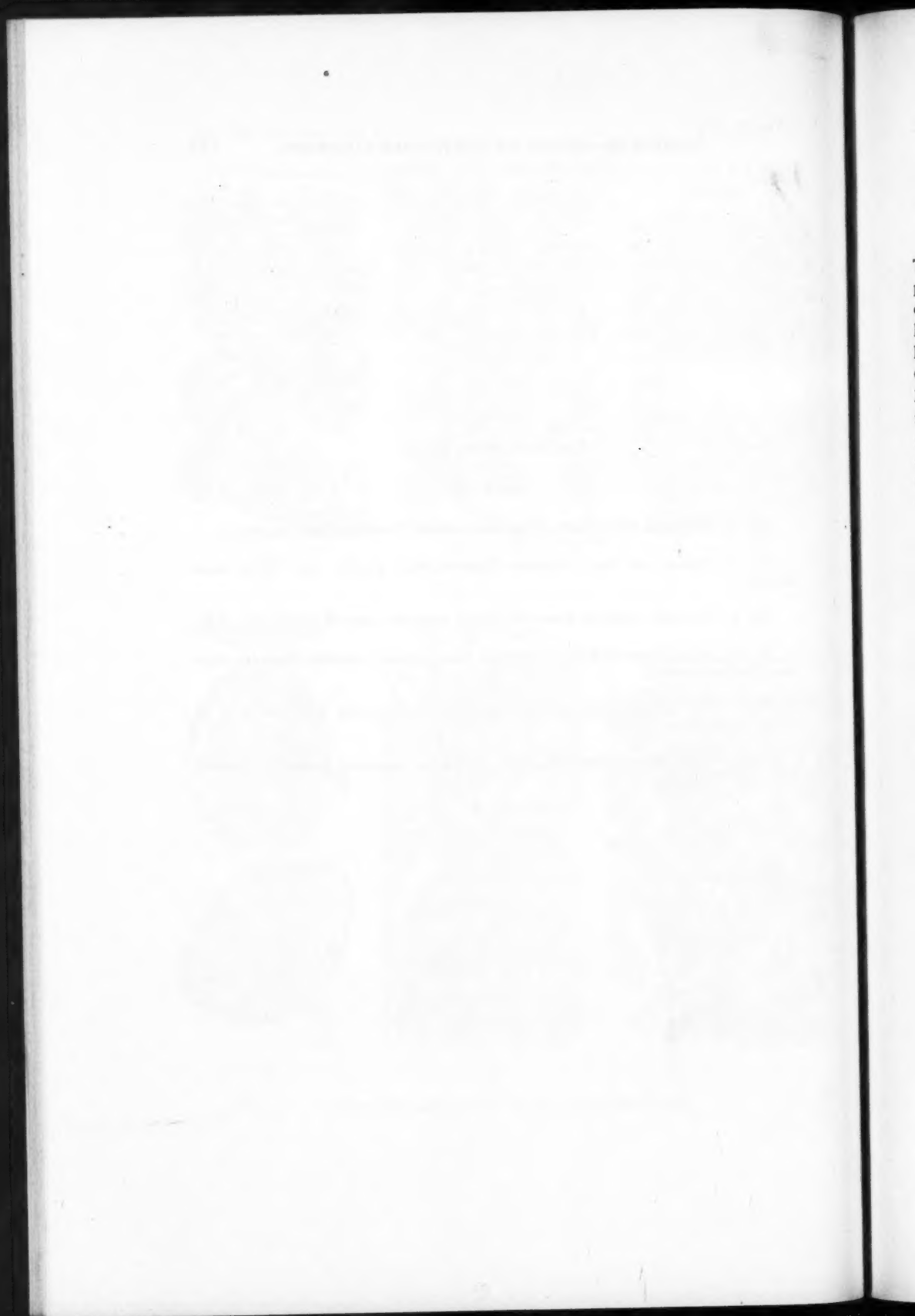


6

EXPLANATION OF PLATE

PLATE 12

- Fig. 1. *Cucurbita indica* from Matthioli, probably *Cucurbita Pepo*.
- Fig. 2. *Pepones lati* from Dodoens—*Cucurbita Pepo*, possibly var. "White Bush Scallop."
- Fig. 3. *Cucurbita verrucosa* from Daléchamps, evidently a warted variety of *C. Pepo*.
- Fig. 4. *Melo-pepones latiores Clypeiformes* from Lobelius, probably *Cucurbita Pepo* var. "Golden Custard."
- Fig. 5. *Pepo maximus Indicus compressus* from Lobelius—the first illustration of *Cucurbita maxima*.
- Fig. 6. *Pepo Indicus minor angulosus* of Tabernaemontanus, probably *Cucurbita Pepo* var. "Table Queen."



## FOSSIL POLYPORES FROM IDAHO

HENRY N. ANDREWS  
AND LEE W. LENZ

In June, 1946, we spent a day searching for fossil plant remains in the late Tertiary deposits in southwestern Idaho. Our primary quest in this region was for petrified evergreen cones that have occasionally turned up, although only in such quantity as to whet the appetite of collectors. The focal point of that day's collecting was approximately 10.5 miles south of Bruneau and .5 mile east of state highway No. 51 which runs south from Mountain Home, Idaho, through Owyhee County into Nevada. In the course of the day one member of our party, Mr. J. M. Dodds, a County Commissioner, of Boise, discovered a fine specimen of a petrified polypore. More recently, Mr. S. H. Osgood, of Rupert, Idaho, has sent us a fragment of another specimen. Although both of our specimens seem to be clearly referable to the fossil *Fomes idahoensis* Brown (Brown, '40), in view of the great rarity of fossil polypores a brief record of the specimens seems worth while.

This part of Idaho is well known to local mineral collectors for its abundance of fossil wood, as well as the occasional cones. Most of these fossils are weathering out of a loosely consolidated, fine white sandstone which is overlain by a brownish-buff sandstone of a harder texture likewise yielding petrified plant remains. Overlying the productive plant beds is a horizon which yields an abundance of well-preserved fish jaws (*Mylocyprinus robustus* Leidy). The only stratigraphical study of the beds in this region is that of Piper's ('24), and the horizon from which our fossils were obtained was apparently in his group No. 8 which is described as "Lake sediments, semi-consolidated, white, gray, and buff sandstones and sandy shales, volcanic ash; . . .". These beds have been considered to be of Pliocene age although it is possible that they may be of later origin. In a recent letter (February 20, 1947) Dr. Bobb Schaeffer has informed us of a collection of *Mylocyprinus robustus* fossil fish pharyngeals in the American Museum that were collected "from an area in southwest Idaho between 'Catherine and Sinker Creeks.' This particular locality is considered to be Pleistocene and as this genus has not previously been reported from older formations I am wondering if your horizon might not also be referable to that period."

### POLYPORACEAE

*Fomes idahoensis* Brown.—The Dodds specimen is a nearly complete sporophore, only a small portion of one side having been lost. As seen in top view (fig. 1) it measures 10 x 11 cm. It bears but one layer of pores, which are 12 to 15 mm. long and number approximately 720 per square cm. Judging from the portion remaining it did not attain a thickness exceeding 2 cm. The rings of growth, characteristic of the living bracket polypores, are clearly defined on the upper surface. While it is not sufficiently well preserved to reveal any significant

diagnostic characters, a longitudinal ground thin section reveals a fine filamentous structure suggesting mycelium. The specimen is preserved as No. 5000 in the collections of the Henry Shaw School of Botany.

The Osgood specimen (No. 5001) is a fragment of an appreciably larger polypore that was probably about 15 cm. in diameter. The pores of this specimen attain a length of slightly more than 20 mm.

The primary interest in these fossils lies in their evident position in the Polyporaceae, and within this family they appear to be most closely related to the genera *Fomes* and *Polyporus*. Their general aspect is that of a *Fomes*, and because of the close resemblance to *Fomes idaboensis* we have assigned them to that species. The lack of dependable color preservation in these, as in most fossils, detracts appreciably from making an entirely dependable comparison with modern species of *Fomes* and *Polyporus*. Brown has, however, noted a rather close similarity between *F. idaboensis* and the living *F. pinicola* (Sw.) Cooke.

Only two undoubted American fossil polypores have been recorded previously. Mason ('34) has described a specimen of *Fomes applanatus* (Pers.) Gill. from the Pleistocene Tomales formation of Tomales Bay, California. Brown's specimen of *Fomes idaboensis* was collected about 5 miles north of the Bruneau locality from which our specimens were found.

We wish to thank Mr. J. M. Dodds and Mr. S. H. Osgood for kindly presenting these fossil fungi for preservation in the Henry Shaw School of Botany collections. Thanks are also due Dr. Bobb Schaeffer, The American Museum of Natural History, for identifying the fossil fish pharyngeals as being referable to *Mylocyprinus* and probably the species *robustus* of Leidy. Through the courtesy of Dr. R. W. Brown we have been able to compare our specimens with a portion of the type specimen of *Fomes idaboensis*.

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#### EXPLANATION OF PLATE

##### PLATE 13

##### *Fomes idaboensis* Brown

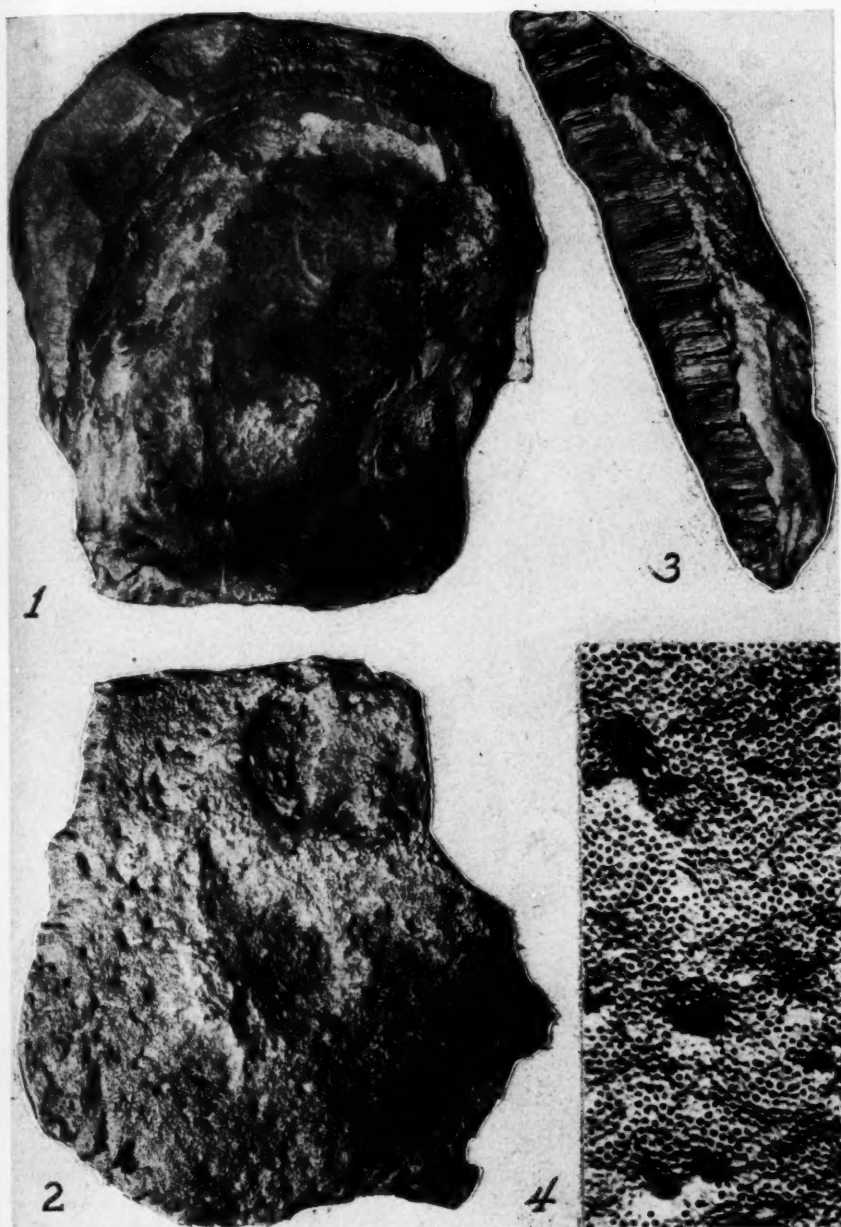
Fig. 1. Upper surface of the sporophore. Pores may be noted where portions of the context have broken away.

Fig. 2. Under surface.

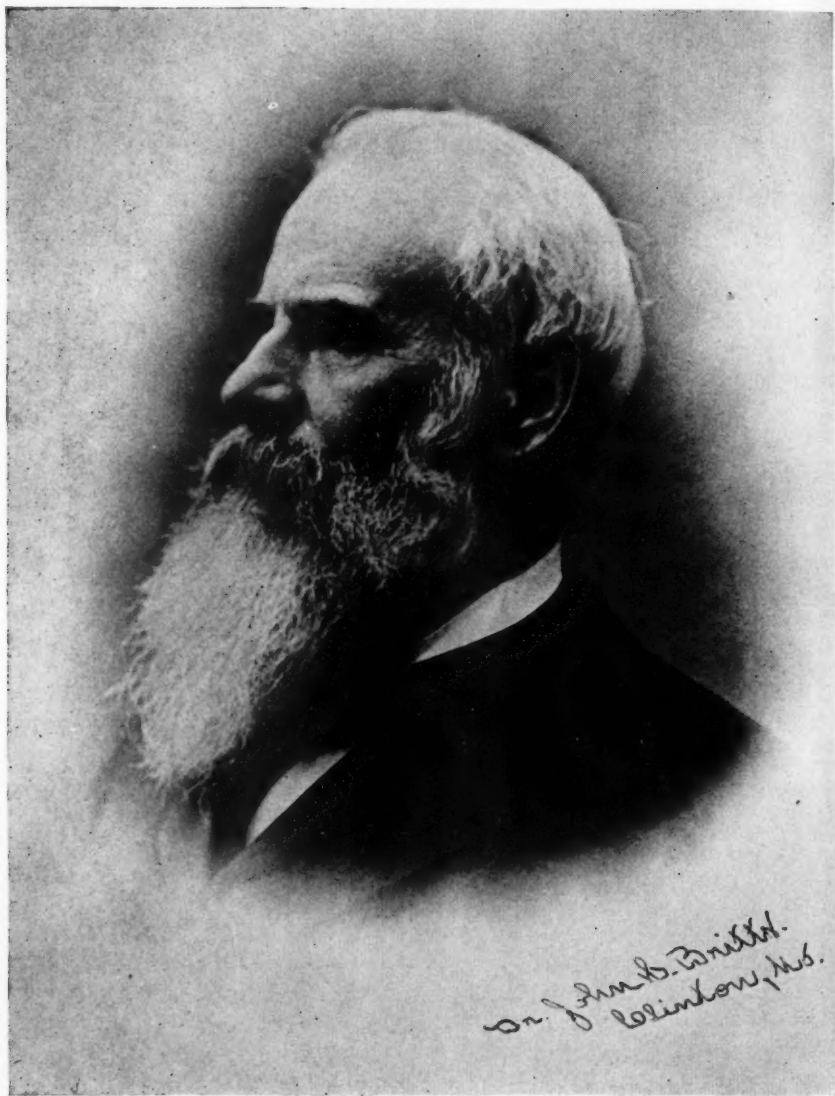
Fig. 3. Side view showing the single layer of pores.

Fig. 4. A portion of the under surface showing the pores enlarged.

Figures 1-3 nearly natural size. Figure 4 magnified 4 times. All photographs of specimen No. 5000.



ANDREWS & LENZ—FOMES IDAHOENSIS



DR. JOHN HENRY BRITTS

November 1, 1836—November 15, 1909

## JOHN HENRY BRITTS—PHYSICIAN AND FOSSIL HUNTER

HENRY N. ANDREWS

In 1899 the United States Geological Survey published a classical volume on the Carboniferous fossil plants of the western Missouri region. The author of this work is the late David White, a noted and able geologist and paleobotanist, while behind the scenes, contributing the fossil plants that made it possible, worked a country physician of Clinton, Missouri, Dr. John Henry Britts.

The daily routine of Dr. Britts' life appears to have been no less crowded than is usual for men in his profession, although it was somewhat more colorful, judging from the variety and scope of his undertakings. In addition to his successful medical practice he found considerable time to serve the state in capacities of very lasting benefit. One of the most significant of these is the part he played in revealing the floral splendor of Missouri as it existed some 250 million years ago. But before mentioning in detail these more purely scientific achievements it may be well to briefly sketch in the background of his earlier life.

John Henry Britts was the eldest, and only son, of six children born to his parents, George Mathias Britts and Mary Jane Rogers Britts. His great-grandfather, Adam Britts, emigrated to this country from Germany about 1754, settled in Franklin County, Pennsylvania, and later moved to Virginia about the time of the Revolution. George M. Britts moved from Virginia with his parents apparently at about the turn of the 19th century and located at Ladoga, Indiana. He studied medicine and practiced in Parke and Montgomery counties until the year 1842. The son, John Henry Britts, was born November 1, 1836, in Montgomery County, Indiana. He attended the state schools until the age of 19, when he began the study of medicine. At that time he went to live with his maternal grandfather, Dr. Henry Rogers, with whom he remained until the spring of 1857, when he moved with his family to Clinton, Missouri. He then resumed his study under the preceptorship of his uncle, Dr. John A. Rogers, and during the college year 1857-58 attended lectures at the St. Louis Medical College. It is thus quite evident that he hailed from a family in which the medical tradition was well established, and in view of the scientific interests that he displayed through life it is not surprising that he followed this course at the outset. His formal training certainly was not extensive as compared with modern concepts, yet his learned relatives imparted to young Britts a sound and comprehensive scientific foundation, judging from the success and distinction that he later achieved.

Shortly after Dr. Britts began the practice of medicine in Cass County in 1859 Governor Jackson issued a call for troops to repel the Federal invasion of Missouri. Britts responded and proceeded to raise a company of which he was made Captain. Six months later he joined General Price's army at Springfield and helped to organize Waldo P. Johnson's battalion, which became later a part of the Fourth Infantry Regiment of the Confederate States Army. Dr. Britts was made surgeon of the

regiment with the rank of Major, later being promoted to Brigade Surgeon. On June 9, 1863, while on duty at the City Hospital during the siege of Vicksburg, he was wounded by a shell thrown into the city by Porter's fleet, and it was found necessary to amputate his right leg. The following August he left Vicksburg, a paroled prisoner, and after his recovery served as surgeon in Alabama and Georgia until the end of the War. Upon his return to Clinton in 1865 Dr. Britts formed a professional partnership with Dr. P. S. Jennings which lasted until the death of the latter thirty years later.

Dr. Britts' practice, like that of most physicians working in small cities and towns, extended over a wide territory. It was this frequent local travelling, combined with an intense scientific curiosity, that made possible the accumulation of his collections of fossil plants. At that time many coal mines were operating in Henry County and the adjacent territory, and Dr. Britts often visited them. Along with his medical kit, he always carried in his buggy a bag of tools, including pick and hammers, to carve out a few choice specimens from the shales that the coal miners laid aside for his study.

In addition to the numerous specimens that he furnished to private individuals and public institutions a large collection of Dr. Britts' fossils were placed many years ago in the Chicago Academy of Science's Museum. Mr. Eliot C. Williams, Jr., has kindly given me the following information concerning these specimens:

"The accession record shows that on May 12, 1904, the Academy received a collection of 1124 coal plants collected by Dr. John H. Britts, in Missouri and Pennsylvania. This gift was made by Mr. Francis Peabody. A notation in the accession record states that the collection contains many types."

"I have checked on the collection, and it seems to be in good shape, but I did not count to see whether or not there are still 1124. I would judge that the collection is probably intact."

"A label in one of the cases indicates that this collection was the basis for Monograph #37 of the U. S. Geological Survey on the Fossil Flora of the Lower Coal Measures of Missouri, by David White." (Letter dated July 18, 1946.)

Dr. Roland W. Brown has informed me that the U. S. National Museum houses approximately 1,000 of Dr. Britts' specimens from the Missouri Coal Measures. Many of these are type and figured specimens. I have not had occasion to study these two important collections of American Carboniferous plants, although it is believed that paleobotanists working in this field would be glad to know of their whereabouts. Apparently the two collections contain all of the types in the above-mentioned Monograph.

Following the publication of the Missouri Monograph Dr. Britts continued collecting plants from the coal mines. Most of the specimens composing this later collection were acquired during or shortly prior to 1904. It was through the kind offices of Mr. D. K. Greger, formerly a curator of paleontology at Washington University, that the existence of this collection was brought to my attention some eight years ago. At that time it was in the possession of a grandson of Dr. Britts, Mr. J. B. Owen of Clinton, from whom it was later purchased for Washington University in St. Louis. It is not a large collection, but a considerable

portion of the specimens are of exquisite beauty both in their preservation and scientific and teaching value. It is especially rich in fine examples of *Asterophyllites* and *Annularia*.

Most of the mines from which these fossils were acquired have long since closed, and it is questionable whether it will ever again be possible to continue where Dr. Britts left off. At least we have a reasonably representative selection of the plant fossils from his old hunting grounds which will always serve as an invaluable foundation for such paleobotanical studies as may be carried on in that region. Our knowledge of Carboniferous floras is increasing every year as new regions are opened up and old ones reworked, and it is largely through the efforts of such active amateur workers that this knowledge is forthcoming.

Thanks are due Mr. John B. Owen for placing at my disposal biographical data pertaining to his grandfather.



# THE IDAHO TEMPSKYAS AND ASSOCIATED FOSSIL PLANTS<sup>1</sup>

HENRY N. ANDREWS

AND ELLEN M. KERN

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## HISTORICAL INTRODUCTION

Very few fossil plants have ever presented a more distinctive anatomy or more challenging problems than the Cretaceous Tempskyas. It is perhaps well to point out in these first few lines that we do not pretend to have arrived at a final accounting of all the existing gaps in our knowledge of these ferns. However, certain significant facts have been discovered concerning their habit and the plants associated with them in life which will stand unchallenged, while our interpretations may raise doubts or be modified by future investigations. It is intended that this should be taken as simply another chapter in our growing knowledge of the Tempskyas.

Through a most fortuitous circumstance that has been described elsewhere (Andrews, '47) I was able to comb certain of the hills in southeastern Idaho<sup>2</sup> in

<sup>1</sup>This study was aided by a grant from the Penrose Fund of the American Philosophical Society.

<sup>2</sup>Collecting activities were carried on by the senior author and certain persons in Idaho whose names are given in the Acknowledgments and elsewhere in this paper.

the early summer of 1942 under the guidance of Mr. W. A. Peters of Jerome, Idaho, chiefly in search of petrified trunks referred to the genus *Tempskya*. In a technical paper it may seem out of order to dwell on an introduction to the subject at hand, yet there are so many details of botanical, historical, as well as general human interest, attached to this group of plants that we believe they should be recorded for the benefit of those who may continue with studies of this and other plant groups in Idaho.

In the summer of 1939 I was presented with a small fragment of a *Tempskya* which had been collected in a gravel pile near the Haddenham fossil shop at Fossil, Wyoming. At that time even a fragment seemed like a treasure—it meant material for class study, but, of greater importance, it meant that *Tempskyas* should be found in much more abundance near by. In later years we traced the probable origin of that fragment to an Upper Cretaceous horizon running north and south a few miles to the east of Kemmerer, Wyoming. It was not, however, until an abundance of large, well-preserved specimens were found in the adjoining Idaho hills that we became fully aware of the importance of these plants in the Cretaceous vegetation.

Through an intimate knowledge of their countryside, a number of local collectors have enabled us to acquire a considerable quantity of specimens. The vigorous collecting activities of Mr. C. Henry Thomas, of Wayan, Idaho, and Mr. E. Manion, of Firth, should be noted in particular. Among the numerous westerners whose acquaintances have enriched my life and laboratory the name of Henry Thomas should be recorded as a great collector and a *Tempskya* specialist. In his assiduous search for these fossils he may be compared only with Wieland, who collected cycads in the Black Hills, or the early bone hunters such as Sternberg or Hatcher. It is a comparison on a smaller scale and of a somewhat more specialized nature, but the pioneering spirit and prodigious productivity differ but little.

My first contact with Mr. Thomas was in 1942, when he still occupied his former ranch on the Williamsburg bench area. I was not prepared to lunch in these rather remote though beautiful hills with a rancher whose cabin was lined with hundreds of books. While lacking the literary capacities of a Thoreau it was soon evident that here was a man who understood and appreciated the world he lived in. At the rear of Mr. Thomas's cabin a wooden platform already displayed scores of fine *Tempskyas* collected mostly within a radius of a few hundred yards. Encouraged by Dr. Roland W. Brown and myself, Mr. Thomas set to work scouring the near-by hills with increased interest and enthusiasm, with the result that the collection has been increased manyfold, consisting now of some few tons of fine specimens, in all probability far more than in all other collections combined (fig. 2). Believing that the *Tempskyas* are destined to occupy an important niche in Cretaceous floras, I requested Mr. Thomas to write in his own words a few lines pertaining to his discovery of the fossils in this region. This has been included in the Appendix for such historical interest as it may have for future paleobotanists.

## THE PRESENT STATUS OF OUR KNOWLEDGE OF TEMPSKYA

Although petrified trunks belonging to the genus *Tempskya* were discovered well over a century ago in Europe, the first really informative accounts of these plants were those given by Kidston and Gwynne-Vaughan in 1911, and Seward in 1924. More recently Read and Brown ('37) and Read ('39) have given us much more comprehensive treatments. A detailed review of previous contributions is included in their account and will be repeated here only in so far as is necessary to orient the reader and to compare our findings and concepts with those of previous workers.

It is especially important to note that prior to Read and Brown's important work all descriptions had been based on either very poorly preserved specimens or a few fragmentary ones. The only possible exception to this statement is Seward's description of *Tempskya Knowltoni* from the Colorado shale of Montana. A detailed consideration of that specimen will be taken up later. This historical aspect of the subject is particularly significant in the case of *Tempskya* for its anatomy is so peculiar as to lead to highly erroneous conclusions concerning the habit of the plant unless adequate material is available for study.

Six species of *Tempskya* have now been described from North America. These include a specimen from Maryland described by Berry in 1911. According to more recent workers this was very poorly preserved and is of little interest or importance other than as a geographical record for the genus. Later Seward described his *T. Knowltoni* from Montana, and in 1937 Read and Brown described two more species and recorded specimens from a considerable number of localities in Wyoming, Idaho, Utah, Montana, and Oregon. Most recently Arnold ('45) has described two more species, *Tempskya Wesselii* and *T. wyomingensis*, from Montana and Oregon, and Wyoming, respectively. Combined with the previous European reports which record specimens from Russia, Bohemia, and England, the wide distribution of these plants in Upper Cretaceous times is well established.

We should like to emphasize that our own studies have not been primarily of a taxonomic nature. We are inclined to doubt that certain of the better-known American species are sufficiently distinct to warrant the specific names that they bear but with this phase of the *Tempskya* story we have no quarrel or primary interest. When dealing with anatomical characters it is not always possible to arrive at entirely satisfactory criteria for the segregation of species. In the rather large quantity of material that we have had available for study there is considerable variation in the gross form of the trunks, but with the exception of a very few specimens it has seemed most feasible to assign all of these to one species. Our efforts have been directed primarily toward arriving at a clearer concept of the general habit of the plants, their ontogenetic development and physiology. In pursuing this course we have perhaps tended to put less emphasis than previous workers on the segregation of species. However, in view of the undeniably close relationship of the species of *Tempskya* we do not feel that our approach has materially slighted a sound taxonomic treatment. While we have sectioned many

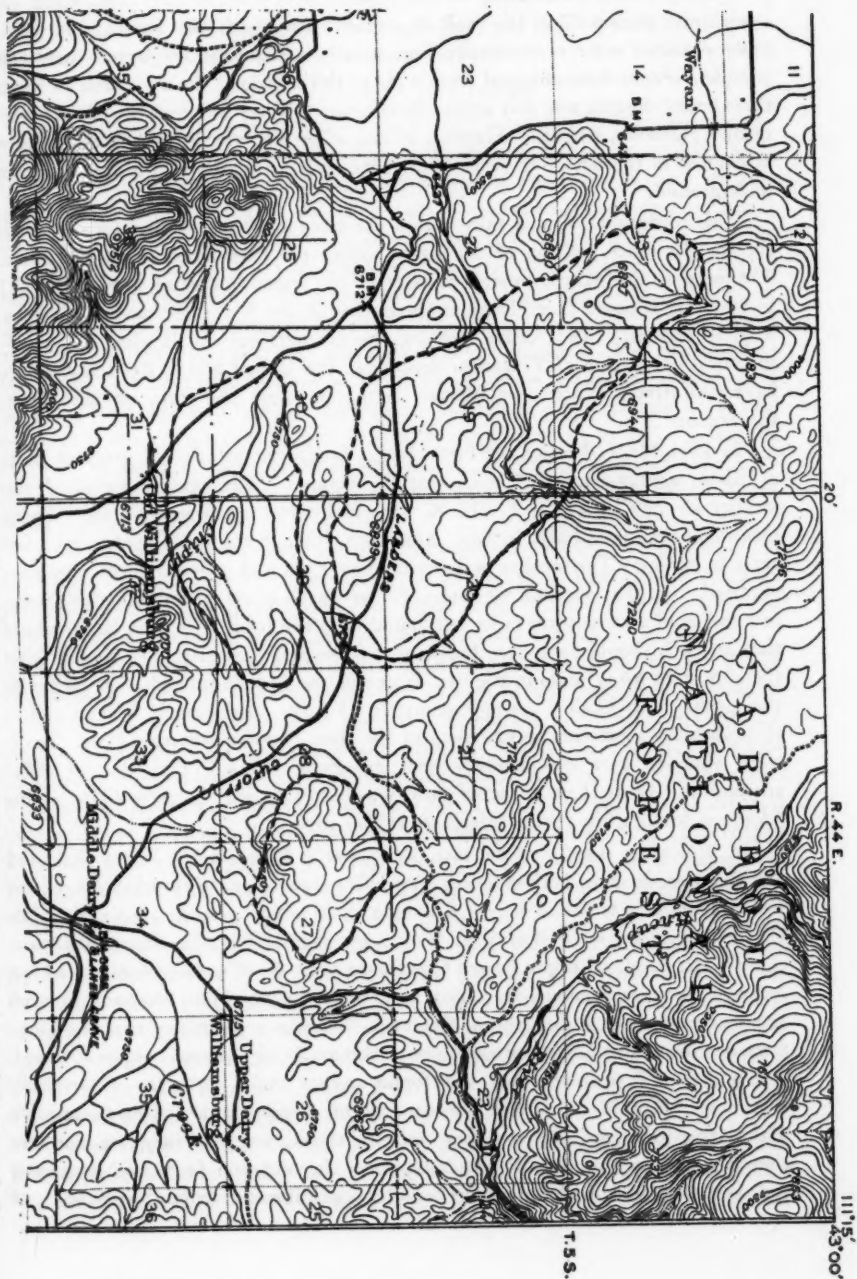
specimens through a wide variety of size and shape, a great many others, particularly the larger ones in the Thomas collection, have not been available for this purpose. We believe that we have studied in cellular detail an adequate number of representative specimens, and from scores of others we have drawn information concerning the habit of the plants. There is obviously some practical limit to the number of specimens that can be handled, and with some field experience with the *Tempskya*s one may select representative material with a minimum danger of missing essential details.

A typical transverse section of a *Tempskya* trunk reveals a most unique anatomy. It consists of numerous, small, siphonostelic stems held firmly together in a dense matrix of diarch roots (figs. 24, 28). Taken individually, the anatomy of a single stem is not unlike that of a modern maidenhair fern (figs. 20, 21, 22), such as *Adiantum pedatum*, while leaf traces are given off in two rows toward the nearest external point of the trunk (text-fig. 2). This unit aggregation of many branching stems with their petioles and roots has been called a "false-stem" by previous writers. It is, we feel, a superfluous term as well as somewhat misleading. If a special term must be used it would be more appropriate to call it a "super-stem," and while an adequately descriptive phrase would be cumbersome, we have preferred to use the term *trunk* as one that involves no new creation and can hardly be misinterpreted.

In order to define clearly the objectives in our own study it may be most expedient to note the chief gaps in our knowledge of these fossils. Sufficiently large collections had not been available for study to settle many of the concepts concerning the habit of the trunk—whether it was creeping, ascending, or upright. Read ('39) has discussed this in some detail in an interesting and critical paper. The ontogeny of the trunks, their unique physiological set-ups, and the manner in which the foliage was borne present problems that have been but partially explained. It is to these categories that we have been especially drawn. Furthermore, previous work on *Tempskya* has offered but little evidence of the kinds of plants that were associated with them in life. We have been fortunate in finding in the Wayan, Idaho, district the fossil wood of a conifer, a dicotyledon, as well as a cycad specimen with the silicified fern trunks.

#### THE LOCALITIES, AGE AND AREA

The greater part of the *Tempskya* specimens in our collection and all of those in the Thomas collection were obtained from an area of a few square miles immediately east of the Wayan post-office. In order to show this area precisely we have reproduced in text-fig. 1 the northeast corner of the United States Geological Survey's topographic map of the Lanes Creek quadrangle. Although the silicified trunks have been gathered over the greater part of this territory the most productive areas are shown within the dotted lines. Most of the collecting that has been done has been simply a matter of exploring the surface of the hillsides and small stream beds. Excellent material is obtained in this way, and in most cases the specimens show no evidence of long transport either before or after fossilization.



Text-fig. 1. The northeast corner of the Lanes Creek Quadrangle, Idaho, showing, in heavy dotted lines, the areas from which most of the *Tempskys* specimens have been collected in this region. Reproduced by permission of the United States Geological Survey.

During a week's collecting in the autumn of 1945 two days were spent excavating in section 27 in the bank of a draw from which Mr. Thomas had previously obtained some exceptionally fine material. Many of his 'largest and most complete trunks were obtained from a pit at this location. In the course of about three hours' digging one may expect to take out as many hundred pounds of specimens. However, with the exception of one other pit, very little digging has been attempted in this area. It seems likely that large quantities of the fossils remain underground.

This topographical area falls within the bounds of the Wayan formation although the exact position of the latter within the Cretaceous is still uncertain. The most detailed stratigraphical account of the region is that of Mansfield ('27) in which it is noted that "Definite correlation of the Wayan formation is impossible at present." In a chart showing the geographical distribution and stratigraphical correlation of *Tempskya* deposits in the United States, Read and Brown have tentatively placed the Wayan formation near the base of the Upper Cretaceous.

In 1942 Mr. E. Manion, of Firth, Idaho, kindly guided a small party of us to a hillside approximately 25 miles east of Ammon. The exact position of this locality is: NW  $\frac{1}{4}$  sec. 5, T. 2N, R. 41E, Hell Creek quadrangle, Idaho. Specimens have been found here in some abundance although the area is limited to a few acres in extent. The locality was revisited in 1946 and a dozen small specimens obtained. On that occasion we continued our search in the surrounding hills within a radius of two or three miles but found no other fossils. It is to be wondered that any one should have ever happened on this small outcrop, yet we feel that there must be many more in the vast extent of the Cretaceous beds that go far to the south. This locality lies approximately 35 miles northwest of Wayan and in all probability represents an extension of the same *Tempskya*-bearing beds. Specimens obtained here are generally well preserved although they do not differ anatomically from those collected near Wayan. This will be referred to as the "Ammon locality" in future references in this paper.

In Wyoming, shortly to the east, *Tempskya* is found in the Aspen shale and the Thermopolis shale, both of lower Upper Cretaceous age. *Tempskya Knowltoni* from Montana was found in the Colorado shale which extends into the middle Upper Cretaceous, while Berry's *T. Whitei* was derived from the Patapsco formation in Maryland, of upper Lower Cretaceous age. *T. Wessellii* (Arnold, '45) is reported from the Kootenai formation northwest of Great Falls, Montana (as well as a placer outwash at Greenhorn, Oregon). There is a possibility that the Montana specimens may have weathered out of the overlying Colorado group (Arnold, '45, p. 26). *T. wyomingensis* was found twenty miles northeast of Greybull, Wyoming. Arnold notes that "Fragments of *Tempskya* are widely scattered within the valley of Beaver Creek and its tributaries, but they are nowhere abundant. They have been found only where the Morrison formation is exposed and are associated with enormous numbers of dinosaur bone fragments and

gastroliths;".

It is thus clear that the *Tempskyas* ranged from the upper part of the Lower Cretaceous through middle Upper Cretaceous times.

#### SIZE AND FORM OF THE TRUNKS

With only one or two exceptions all the *Tempskyas* specimens that we have examined from the Wayan and Ammon localities compare most closely with *Tempskyas Wessellii* Arnold. Although the following discussion is based on this species unless otherwise noted, the views that are expressed concerning its habit, ontogeny, and physiology are probably generally applicable to the genus as a whole.

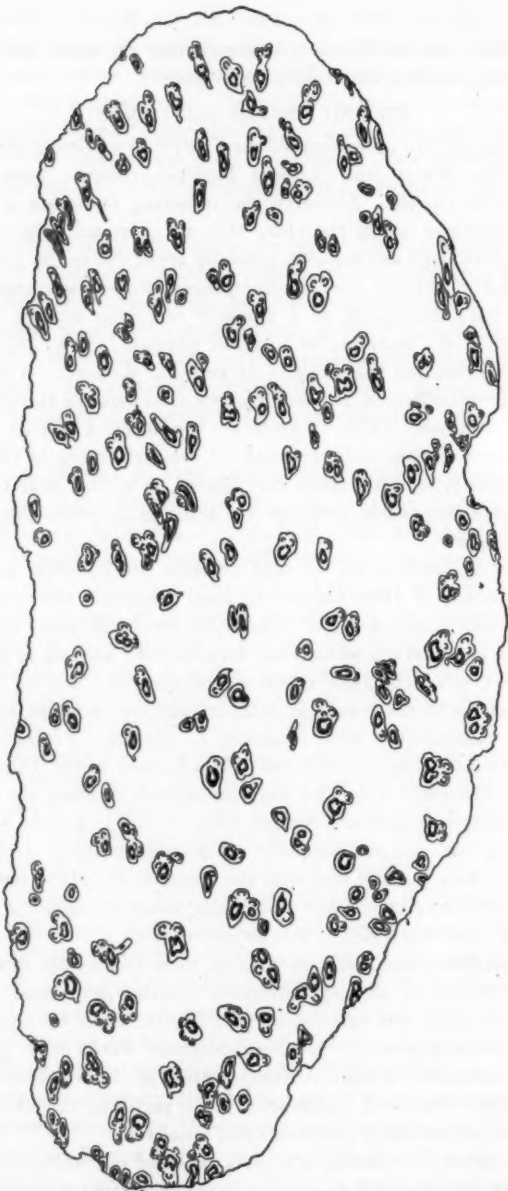
Some concept of the size that the *Tempskyas* attained was known as early as 1836 from Fitton's description of a trunk 9 feet long and 12 x 4 inches in diameter, found in the southeast of England (Stopes, '15, p. 14). Much more recently Read has reported trunks up to 10 inches in diameter. The largest specimen in the Thomas collection, and so far as we are aware the largest yet reported, is 16 inches in diameter. Other fragmentary specimens, which do not constitute complete transverse sections, indicate trunks of even larger size, so that a maximum of 18 or 20 inches in diameter seems very likely. It is thus clear that these were plants of no mean magnitude, although the evidence indicates that they did not attain a great height.

As a matter of convenience we shall consider the hundreds of specimens in the Thomas collection in three categories: basal specimens, tips, and intermediate portions which will be called *discs*. This latter term will apply to any specimen that is complete in transverse section but may be quite variable in length.

*The bases*.—One of the chief objectives of the 1945 trip to Wayan was to obtain basal portions of the trunks in order to shed further light on their general habit; that is, whether they were ascending or upright. Fortunately some fine specimens were collected in the field and others located in the Thomas collection. In all cases the specimens which we have interpreted as being the basal portions flare outward slightly at the very bottom (figs. 3, 5, 7), present a characteristic knobby lower surface, and are composed exclusively of roots. It is apparent, as Read and Brown have pointed out, that the stems in the older, basal portions of the trunks decayed completely, their place being taken by roots. A more detailed discussion of the anatomical details will be given later.

The basal periphery and under surface of these stumps are distinctive. The former is characterized by slightly buttressed, rounded projections and the latter by slightly raised knobs and cavities, or in a few instances by one large shallow cavity. The general uniformity of these specimens would seem to support the view that they represent the original stump portion of the trunk and not simply a broken sector taken from some higher level. It is pertinent to add, therefore, that they are all upright, indicating perfectly erect trunks.

One cannot be certain whether the roots extended out uniformly in all directions or whether they tended to aggregate into more massive "compound roots." The knobby character of the extreme base may point to the latter explanation



Text-fig. 2. A diagrammatic drawing of a transverse section of specimen T38 (peel 14) showing the distribution of the stems and the position of the xylem of stele and petiole traces. It may be noted that stem branchings are numerous and the trunk is radially symmetrical with respect to departure of the traces. Natural size.

although this is offered only as a suggestion. An objection may be raised that these small almost microscopic roots (pls. 20, 21, 24) could not have adequately anchored such a massive trunk. When it is considered, however, that they probably radiated out by the tens of thousands, that at some points they may have been aggregated to form compound roots, and that the individual roots possess an extremely stout sclerotic cortex (fig. 19, etc.), there can be no doubt that their supporting capacity was very great. Another objection may be raised that this knobby surface is an erosion artifact caused either before or after fossilization. However, the sides and upper surface of these specimens show no such effect, and the stumps always flare outward slightly at the extreme bottom, as might be expected.

*The disc specimens.*—The specimens that we have interpreted as being basal and terminal portions of trunks are considerably in the minority, which indicates that the plants did attain a height of at least some few feet.

If the cross-sectional form of these disc specimens could be depended upon as a specific taxonomic character the number of species represented would be very nearly endless. Different specimens vary from circular, to broadly elliptical, to strongly flattened in transverse section (figs. 10, 24, 25); and one specimen was found in which the trunk is crescent-shaped (fig. 9). Since we have not been able to observe any correlation between these variations in form and the internal structure of the trunks, such variations would seem to be of no taxonomic significance. It is possible that the variously flattened specimens have resulted from crushing caused by overlying sediments prior to silicification. A more detailed anatomical consideration bearing on this problem will be given on a later page.

The size and form variation of some specimens in the Thomas collection is recorded in Table I, this information having been compiled chiefly with the view of arriving at some concept of the height that these plants attained. In compiling these data a representative selection of specimens has been taken, all of which were complete in transverse section. Many more might have been added to the list, but in general they would have affected only the quantitative aspect of the table.

Since none of the specimens represents a complete trunk we cannot arrive at an exact figure for the height of a plant in life; however, from many observations of their diameters and the rate of tapering we may calculate a reasonably dependable minimum. In the cases of the base and disc specimens we have recorded the diameters at both ends in order to indicate the rate of taper. Of the terminal trunk specimens only the basal diameter can, of course, be given.

An examination of these figures for the trunk (disc) specimens will show that none of them taper abruptly from one end to the other. Such tapering is found only in the undoubted terminal specimens. The longest one that we have observed is in the Manion collection (specimen A), from the Ammon locality, and through its length of 21 inches it displays no tapering. The same holds true in a general way for the basal specimens, which flare slightly at the extreme base but otherwise give no evidence that the trunks were very short (figs. 3 and 7).

TABLE I  
MEASUREMENTS OF A REPRESENTATIVE COLLECTION OF TEMPSKYA SPECIMENS

Specimen number*	Nature of specimen†	Diameter (s) in inches	Length in inches
9	Tr	9. x 6.5‡ 11. x 7.	12.3
11	Tr	9.3 x 6 10. x 7.	11.
19	Tr	11. x 10.‡‡	11.
21	Tr	12.3 x 10.5	6.
26	Tr	4.7 x 2.5 6. x 4.	11.
31	Tr	14. x 4.7	11.
32	Tr	8.5 x 6.5 9. x 7.	10.
33	Tr	10.5 x 5.	13.
38	Tr	5.5 x 3.7	6.
39	Tr	3. x 1.7 4.3 x 2.	7.
40	Tr	7. x 5. 8. x 5.5	7.
42	Tr	13. x 7.3	6.
45	Tr	8.7§	11.
46	Tr	6.5 x 6.	10.
47	Tr	5. x 3.3 5.7 x 3.7	7.
48	Tr	9.3 x 5.3 10. x 5.3	9.
51	Tr. (near base)	14. 16.	10.
A (Manion coll.)	Tr	9.	21.5
W. U. (T216)	Tr	6. x 4.5 7. x 5.5	16.
6	B	7. 7.5	8.
10	B	8. x 5.5 9. x 7.	9.
13	B	11. x 7. 12.5 x 7.	9.
22	B	16.7 x 13.	8.
25	B	8.7 x 9.7 9. x 10.	7.
34	B	9.5 x 4. 9. x 6.	15.
41	B	9.7 x 7.3 8.7 x 7.3	10.
43	B	9.5 11.	9.
44	B	13. x 12.	12.
49	B	7. x 4.3 7.5 x 5.5	7.
23	Ti	8.5 x 13.‡‡	12.
24	Ti	10. x 4.5	7.
W. U. (T47)	Ti	6. x 3.7	8.5
W. U. (T230)	Ti	6. x 3.5	12.

\* Specimen numbers refer to the author's field notes, all measurements being taken from specimens in the Thomas collection unless otherwise indicated. † Tr—trunk (disc); B—base; Ti—tip. ‡A slightly elliptical specimen, the figures in the upper and lower lines being for the top and bottom diameters respectively. ‡‡No appreciable taper of the specimen, the top and bottom diameters being the same. §No appreciable taper, and the specimen is cylindrical or nearly so. ¶In the case of tip specimens this refers to the diameter at the base.

In this respect it is necessary to consider the internal structure of the trunks. The densely compacted stems and roots that make up the trunks must have had in life the consistency of a very tough strand of rope. In texture it probably was not unlike an *Osmunda* rhizome with its vast coat of petioles and roots. In the *Tempskya* trunks, however, there were many stems and the whole aggregation was bound together very tightly. Thus while the trunks must have been very tough they were probably not extremely rigid. The thousands of roots created a closely interwoven unit; yet, lacking an interspersed ground tissue, such a height as is attained by a coconut or royal palm would seem to be improbable. One other pertinent point may, however, be mentioned here. Unlike other unbranched, columnar trees such as living palms, tree ferns, and cycads, *Tempskya* bore very small fronds, as is evidenced by the relatively minute size of the petioles, and we shall offer evidence that these were borne not merely in a crown at the top but for a considerable distance down the trunk as well. Thus, in all probability the Tempskyas did not have the mechanical problem of a large weight of foliage concentrated at the top, a feature which allows for a considerably taller trunk than might otherwise be expected.

It may be noted that some of the longest specimens from the Wayan region (Table I, Nos. 33, 34, T216) display but little tapering from one end to the other. The nineteen disc specimens considered in the table all have an average taper of approximately .6 inches per foot. Thus, assuming a uniform taper throughout, a trunk 10 inches in diameter at the base would taper to a point at a height of about 16 feet. This is probably in excess of the height actually attained since, among other factors, the apex of the trunk tapers abruptly to a blunt point (figs. 26, 27). From the terminal specimens at hand we may suppose, then, that at a diameter of 3 or 4 inches our trunk terminated, giving a height of about 12 feet. In view of the relative proportion of basal and terminal trunk specimens along with the discs this figure seems quite reasonable.

The specimen of maximum diameter (#51 in the table) measures 14 and 16 inches at the upper and lower ends, respectively, and is 10 inches long. This had been exposed for some time prior to collection and is somewhat lichen-encrusted. No evidence of stems could be observed in the transverse sections, indicating that the specimen came from near the base of a trunk, although it does not represent the basal-most portion as both end surfaces are irregularly broken. On the basis of the estimate given above for a trunk 10 inches in diameter it is possible that this specimen may represent a plant that attained a height of about 19 feet.

Prior to the publication of Read and Brown's work, accounts of *Tempskya* were based on so few, as well as fragmentary, specimens that a satisfactory concept of the habit of the trunks was not possible. Read has more recently presented a more detailed discussion ('39) dealing with "The evolution of habit in *Tempskya*." While certain of his concepts are clear-cut and sound, we are not able to agree in all respects with his conclusions. Read states, "In short, the writer's concept of the growth form of the dorsiventral false stemmed species of *Tempskya* is an as-

ceding, climbing type of fern with numerous liana adaptations. It is of course obvious that the very basal portions of the stem were horizontal or oblique. However it is doubtful if these subterranean portions developed the dense mass of parallel roots characteristic of the false stem. Rather they must have been markedly divergent." (p. 70).

In the hundreds of specimens that we have collected or studied from the Idaho localities the evidence points toward an upright, self-supporting trunk without liana adaptations, and we cannot agree that it is "obvious" that the basal portions were horizontal or oblique. Our evidence as gained from a study of the external form of the trunks may be considered first.

It seems significant that we have encountered only two specimens (one shown in fig. 8) which show any noticeable longitudinal curvature. Basal specimens give no evidence of other than upright habit from the start.<sup>3</sup> Two concepts that seem to have become indelibly impressed in the minds of those paleobotanists who have seriously studied the *Tempskyas* deserve analysis at this point. The first of these is based on the specimen of *Tempskya Knowltoni* described from Montana by Seward in 1924. That specimen is described and figured as being 33.5 cm. long and obconical in form, the supposed basal end being 1.5 cm. in diameter and the enlarged apical end 6.5 in diameter. It is certainly apparent that a *Tempskya* trunk of such an obconical form would have been mechanically incapable of attaining any appreciable height, and even if it could in such a small specimen as this it must have been dangerously top-heavy. A very likely flaw, however, in Seward's interpretation of this as a complete trunk lies in the anatomy of the specimen. He has indicated (text-fig. 2, page 490) that the trunk is anatomically dorsiventral, that is, the petioles for the most part pass out toward one side. Read and Brown likewise figure *Tempskya minor* as showing predominantly dorsiventral orientation of the stems composing the trunk. We feel that it is very likely that these authors have been dealing, in such cases, with portions of much larger trunks in reaching these conclusions. By sectioning some 70 specimens and preparing peel preparations of the entire transverse surface we observed the course of the stems and petioles. These specimens have ranged from 5 to 30 cm. in diameter, and in nearly every case, whether the trunks were circular or oval in transverse section, the orientation of the stem-petiole organization with respect to the trunk as a whole is strictly radial,—that is, the petioles depart toward the nearest outer point of the trunk. This evidence of radial arrangement is based, furthermore, on trunk specimens that show no indication of appreciable weathering or fracturing. There can be no doubt that they represent complete transverse sections, with the exception of the outermost projecting stem tips and petiole bases. Seward indicates, moreover, that with his specimen "the surface appears to be waterworn." Evidence from a few specimens could thus be very misleading, and fragmentary ones must be expected

<sup>3</sup>In the earliest stages of the sporeling the first formed stem may have been creeping or ascending, but concerning this no information is available.

to display this apparent dorsiventrality. Specimens in our own collection, as well as many in the Thomas collection, would, individually, give this impression if complete transverse sections were not available for comparison. We do not wish to criticize Seward's very excellent anatomical study of the single specimen he had available, but rather we wish to point out the errors of interpretation that may readily result from conclusions based on such limited material. The over-all shape of his specimen also argues most strongly in favor of our view that it is but a fragment, for in all of the Idaho specimens the basal portions are clearly the largest in diameter and taper toward the apex. A more detailed consideration of this feature may best be saved for the following section dealing with the ontogeny of the trunk. (Also see discussion of the living *Dicksonia fibrosa* on page 145).

Bower has shown ('35, fig. 296, 1930, etc.) that in the ferns the young sporophytes are obconical in form, but it must be remembered that this is most apparent during the very early stages. Generally, the stelar system soon attains a maximum diameter as in most of the rhizomatous forms, or increase in diameter is rendered possible by polystely of one sort or another. The ferns have been remarkably adept at modifying their primary stelar tissues to make up for a lack of mastery of the cambium. Such rather divergent structural types as are represented by *Psaronius* and *Tempskya* illustrate the high state of organization that has been made possible. In the case of *Tempskya* we do not know what the very earliest stages in the development were like but there can be little doubt that maximum *individual stelar* size was soon attained and that stelar divisions started very soon after the sporeling stage. Perhaps during the first two or three feet of vertical growth the trunks were obconical, although it is most likely that root development soon counteracted this to produce a trunk that generally tapered from the base toward the apex.

*The tips.*—We have in our own collections three specimens of the terminal portions of trunks, all of which (figs. 26, 27) taper rather abruptly to a blunt apex.

#### THE ONTOGENY OF THE TRUNK AND THE RESTORATION

With the exception of the basal ones, characterized by their anatomical composition of roots and distinctive external features, all the specimens that we have examined display, in transverse section, stems scattered quite uniformly through them, from the extreme periphery to the center. Some specimens show considerably more stems per unit area, which is due, in part at least, to the position of the section, whether nearer the base or apex of the trunk. One of the most striking anatomical features is the short life span of the leaves. It is not possible to indicate precisely how long a frond persisted, but judging from modern ferns, cycads, and palms it probably was not more than one year. The evidence for this lies in the fact that petioles are found only in close proximity to the stem from which they were derived. Thus it would seem that any single stem must have been at the outside of the trunk, terminally or laterally, at the time it was bearing active petioles.

Previous workers have assumed that the *Tempskya* trunks bore a crown of fronds at the top in a fashion generally comparable with that of a modern tree

fern or cycad. The only previously figured restoration is that of Kidston and Gwynne-Vaughan's which appeared in Stopes ('15) Lower Greensand flora. In that restoration a ring of stems is shown composing a sort of compound crown at the top. They are shown branching two or three times, each with a rather dense cluster of leaves. From our observations, such a supposed habit is quite contrary to the evidence afforded by the internal structure of the trunks, as well as the external form of the tip specimens.

The tendency to compare these fossils with modern plants such as tree ferns and cycads is understandable. However, in *Tempskya* we are dealing with a different mode of increase in the diameter of the trunk, as well as a highly unique physiological set-up with regard to photosynthesis and transport of fluids. While most tree ferns, palms, and cycads bear a crown of relatively few, large leaves the *Tempskya*s bore a great many small ones, as is evinced by the minute size of the petiole (figs. 20, 28). It is evident from the dimensions of the petioles, by comparison with those of living ferns, that the fronds must have been very small, probably little more than a foot long. The physiological problem of light relationship where numerous relatively very small fronds are aggregated at the top of the trunk has not previously been given the consideration that we believe is necessary for a reasonable concept of the habit. A quantitative comparison with plants of supposed similar habit will clearly point out the difficulty.

We have measured the trunk and petiole diameters, as well as the number of leaves in a crown, for some cycads, palms, and a low-growing tree fern that are cultivated in the Missouri Botanical Garden greenhouses. The data are presented in Table II, together with those for a few representative specimens of *Tempskya Wesselii*. A comparison of these living columnar-trunked plants, with their crowns of leaves at the top, with the trunks of *Tempskya* reveals certain significant structural divergences. A wide range of trunk types has been purposely included, and of them we may immediately eliminate from close comparison those with tall and uniformly slender trunks and a few large leaves, such as the palms *Hexopetion mexicanum* and *Chamaedorea Tepejilote*. These plants are in no way comparable to the more massive trunks of *Tempskya*. The stouter-trunked forms such as *Phoenix reclinata*, and more especially *P. dactylifera*, present a closer structural comparison. The frond/trunk relationship is, however, worth careful consideration. Two specimens of *P. dactylifera* in our greenhouse measure about 12 and 14 feet high, respectively (up to the crown of leaves), and these have diameters of 14 and 16 inches, respectively, including the very heavy armor of leaf bases, the latter accounting for at least one-third of the trunk diameter. Of particular interest is the base of the petiole which tapers from 4 inches (in its wide diameter) close to the trunk to 1½ inches through a distance of 12 inches. A generally similar organization prevails in the larger-leaved cycads, the basal portion of the petioles being stoutly bulbous to support the weight of the leaf. In all cases we have prepared the petiole/trunk ratio from measurements of the petiole out beyond this

TABLE II

A COMPARISON OF CERTAIN MORPHOLOGICAL DATA IN LIVING PLANTS WITH SPECIMENS OF *T. WESSELI*

Living plants	Ratio of petiole diameter to trunk diameter	Number of leaves in a crown	Remarks
<i>Cycas micboltzii</i>	1:13	15	
<i>C. circinalis</i>	1:11	22	
<i>C. siamensis</i>	1:9	40	
<i>C. revoluta</i>	1:24	16	
<i>Dioon spinulosum</i>	1:9	40	
<i>Encephalartos altensteinii</i>	1:10	12	
<i>Cibotium</i> sp.	1:11		
<i>Phoenix reclinata</i>	1:4	27	Very little taper to trunk, which is enclosed in dense armor of leaf bases.
<i>P. dactylifera</i>	1:10	28	Trunk encased in very dense armor of leaf bases.
<i>Hexopetium mexicanum</i>	1:4	10	No appreciable change in diameter through its 10 feet of height.
<i>Chamaedorea Tepejilote</i>	1:3	4	Very slender clean trunk with little change in diameter through its 8 feet.
<i>Thrinax parviflora</i>	1:2.5	15	Gently tapering trunk, clean below with bulbous base 3" in diameter which tapers to about 3" at departure of first leaf.
<i>Caryota urens</i>	1:2.5	5	Trunk ensheathed with closely appressed leaf bases, uniformly tapering from 5" at ground to 3" where first leaf is given off at height of 6'.
Fossils			
<i>Tempskya Wesseli</i> specimens			
T18	1:30		
T33	1:63		
T51	1:48		
T90	1:39		

great basal swelling. Turning to the *Tempskyas*, in specimen T33 the mean trunk diameter is 170 mm. and the petiole diameter (taken immediately after the departure of the petiole from a stem) is 2.7 mm., the petiole/trunk ratio being 1:63. In comparison with a stout columnar cycad such as *Cycas siamensis* with a trunk 10 inches in diameter (including the leaf bases) and a height of 9 feet, with a petiole 2 inches in diameter close to the base we have a corresponding ratio of 1:5, or when the petiole diameter is taken out beyond the swollen base, a ratio of 1:9 as shown in the table.

The larger-leaved cycads and palms have, as might be expected, an exaggeration of this enlargement of the petiole base to support the weight of the fronds. The relative size of this bulbous base is noticeably smaller in the smaller-leaved species.

Since there is no evidence to indicate that the petioles of a *Tempskya* increased appreciably after their departure from the stem, they must have borne relatively very small fronds. The actual diameters of the petioles in a number of trunks of

*T. Wesselii* immediately after their departure from the stem varies from 1.5 to 2.75 mm. Dimensions of the petioles of cycads (taken immediately beyond the swollen base) range between 8 and 25 mm., those of *Cibotium* sp., 13 mm., and of the palms from 7 to 40 or more mm. Since these figures for the living plants are taken beyond the bulbous base, and the trunk diameters include the leaf base armor, the recorded divergence between their ratios and those of the *Tempskys* is an extremely conservative one.

The Stopes restoration is ingenious in that it allows for a considerable proliferation of the leaf-bearing area. However, the actual terminal trunk specimens do not suggest any such appearance. All the specimens of this nature that we have observed, representative ones being shown in figs. 26 and 27, indicate a rather bluntly tapered apex like that of a living cycad, fern, or palm. In view of the generally good preservation of the Wayan *Tempskys*, most of which show no great wear due to transport either before or after fossilization, we should expect to find some evidence of the stems or at least the rather massive stem aggregates as shown in the Stopes restoration. Such evidence is quite lacking.

A point that we wish to make is that the apex of a *Tempskya* probably could not have borne sufficient photosynthetic surface to have satisfied the requirements of the plant.

From the evidence afforded by internal structure, one of the most striking features of all *Tempskys* trunks (excluding the basal portions) lies in the fact that in any transverse section free petioles are rarely found more than a few millimeters beyond the stem that bore them. In other words (as previous authors have pointed out), the leaves were not persistent for any great length of time.

In order to arrive at a clearer understanding of the mode of lateral growth in *Tempskys* we have: first, observed the stem-petiole-root organization in transverse section in many trunk specimens, varying from approximately 2 to 10 inches in diameter; and, second, followed the course of individual stems in single specimens by means of serial sections. This latter procedure is considered in some detail in the following paragraph.

Two specimens, each approximately 4 inches in diameter,<sup>4</sup> were cut into a series of thin slices in order to determine the extent of branching in the individual stems, their destination, and the number of petioles that depart through a given length. The branching of the stems proved to be so frequent that the slices had to be taken between  $\frac{1}{4}$  and  $\frac{1}{2}$  inch apart in order to follow them with certainty. With reference to stem branching, Read and Brown noted: "The writers attempted to determine the distance between these successive bifurcations by cutting a block several inches long into serial sections, but they found that this character is so variable that it has little value either for morphologic or for taxonomic considerations." (p. 110). While agreeing that the taxonomic value of stem branching

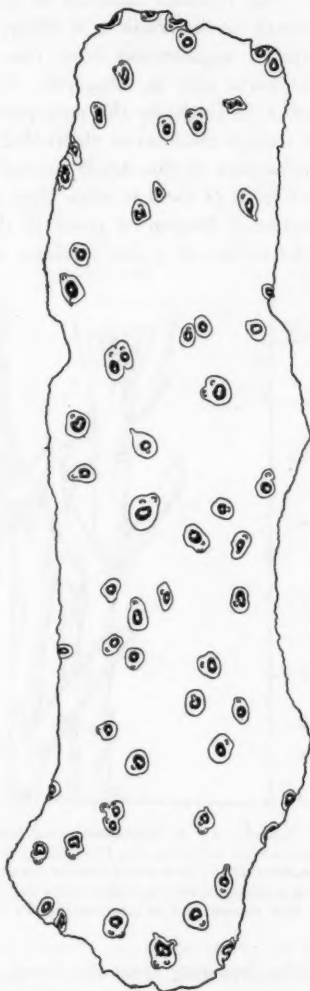
<sup>4</sup>Small specimens were selected for this purpose because of the extreme difficulty of cutting the larger trunks. From a comparison of many specimens varying in size from 2 to 12 inches in diameter there can be no doubt that the branching as described (based on specimens T51 and T90) is representative.

may be negligible we shall try to point out that it is of the utmost significance in an interpretation of the general habit and physiology of the plant as a whole.

It is evident, even without making serial sections, that branching of the stems is very profuse, for in almost any single transverse section of a complete trunk a considerable number of stems may be seen to be dividing. Taking more or less at random complete transverse sections from ten different specimens an average of 45 per cent of the stems was observed to be branching. Thus the serial sections, upon which text-fig. 3 is based, serve to confirm a three-dimensional picture that might have been prepared in a somewhat less exact fashion from a single transverse section. The worth of the peel method has proven an invaluable aid in anatomical studies of this sort. We have not relied upon it exclusively, but it is the only feasible way in which one can prepare complete sections, and often excellent ones, of trunks up to 10 and 12 inches in diameter.

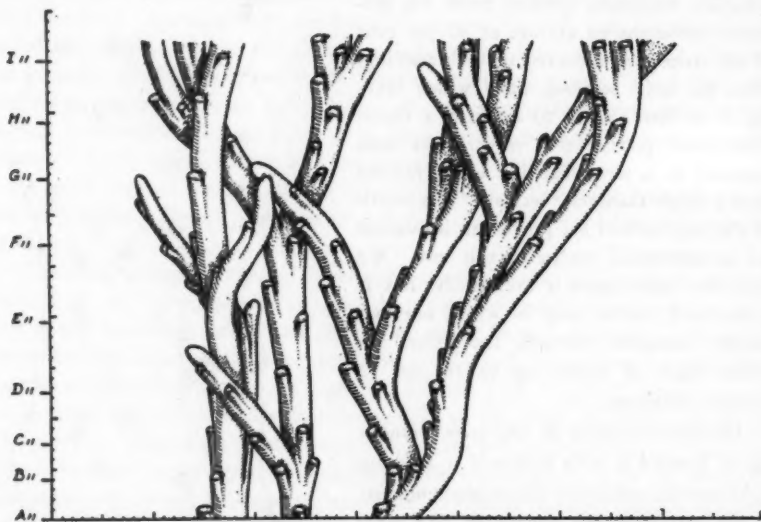
Previous accounts of the stem branching in *Tempskya* have indicated it as being dichotomous, and while this is predominantly the case it is not always so. In some specimens there may be appreciable variation in stem diameters as is shown in figs. 20, 21, and 22.

In order to present a three-dimensional aspect of stem branching we have selected several stems from specimen T90 which have been followed through a distance of 4.5 cm. (text-fig. 4). The average distance between successive divisions is approximately 1.5 cm. This abundant branching activity must result, through any appreciable distance, in either a great congestion of stems, or one of the two divisions soon ceases to grow. The latter is observed to be the case.



Text-fig. 3. A diagrammatic drawing of a transverse section of specimen T2 (peel 13) showing radial symmetry in the departure of the leaf traces in a strongly flattened specimen. Natural size.

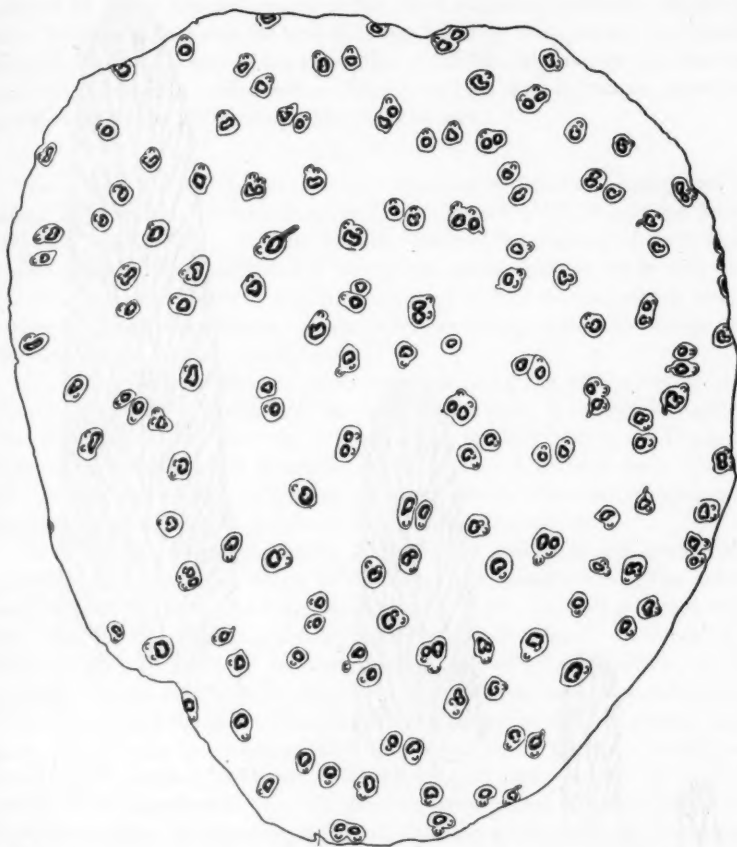
This frequent cessation of growth of many of the stems and the continued growth in the trunk as a whole, by the branches, present a distinctly different type of organization from that of other living or fossil plants with which *Tempskya* may be compared. In *Tempskya* the trunks increase in diameter as well as in height by this same process. While we cannot follow the growth stages of a single specimen in plants that lived 100 million years ago, we can arrive at an explanation of this developmental anatomy by observing trunks of varying sizes, and in all of them it seems clear that increase in diameter has taken place by the continued division of stems at the periphery of the trunk. In virtually every cross-section of a disc specimen stems may be observed (text-figs. 2, 3, 5) ac-



Text-fig. 4. A three-dimensional aspect of stem branching and the production of petioles as obtained by following the branches by means of serial sections, through a distance of 4.5 cm., of specimen T90. Each small division on the horizontal and vertical scales represents 1 mm. In their proper positions on the scale, letters to the left indicate the section, and numbers indicate the peel of that section used in constructing the illustration.

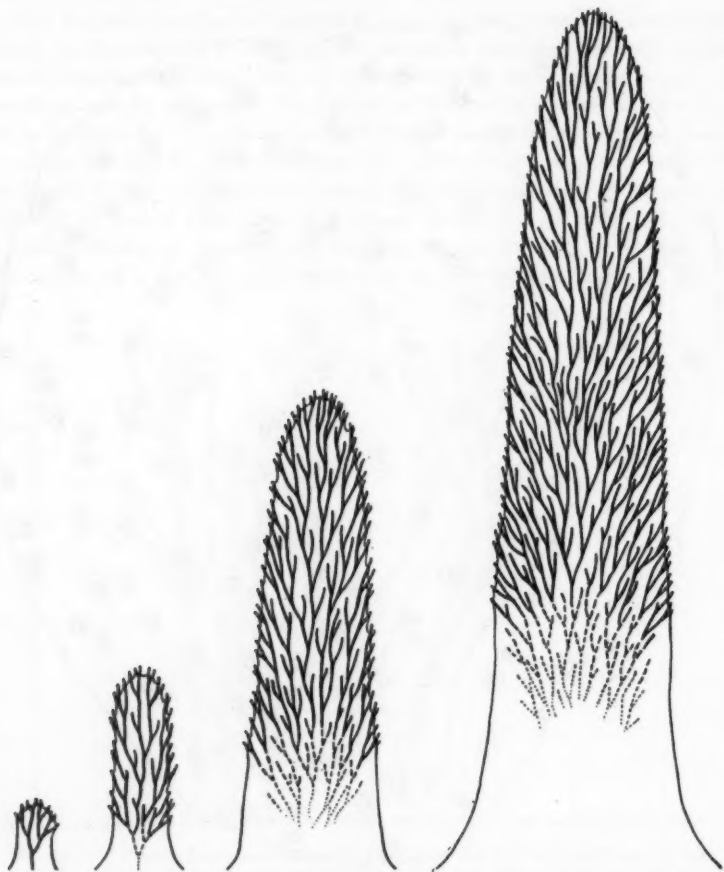
tually departing from the trunk. Just how far these projected out beyond the trunk proper cannot be determined as they apparently were readily broken off during transport prior to fossilization. It is difficult to observe these stems on the outside of the trunk because they departed obliquely and are not readily distinguishable from the roots either laterally along the trunk or at the tip. It is probable that they did not extend more than a centimeter or two at the most, as a greater length would have resulted in excessive crowding of the foliage.

After a short period of growth any individual stem divided, one branch ceased to grow, and the other carried on. We have attempted to show in the series of dia-



Text-fig. 5. A diagrammatic drawing of a transverse section of specimen T226 (peel 3) showing radial symmetry in the departure of the leaf traces in a cylindrical trunk. Natural size.

grams given in text-fig. 6 this apparent mode of growth. As stated above, we have no knowledge of the earliest development of the sporeling but it is evident from the smaller specimens that profuse branching of the stems was initiated very early in the development of the trunk. Just how long the original stems retained direct continuity with the ground likewise cannot be determined. The decay of the stems in the lowest portion was, of, course, gradual and the apical growth continued at a considerably faster pace. However, taking as an example a plant with a basal diameter of 10 inches and a height of 12 feet, it is probable that the lower 2 to 2.5 feet of the trunk was composed of roots (see extreme right diagram in text-fig. 6).



Text-fig. 6. A hypothetical series of longitudinal sections through *Tempskya* trunks showing the supposed mode of growth. The solid lines represent stems, and the dotted lines stems in various stages of decay.

In summary, these seemingly important points may be emphasized: The trunks had a generally tapering form from base to apex; branching of the stems was profuse and apparently uniform throughout the life of a plant, producing lateral as well as apical growth; leaves were not long-persistent and their small size would not have afforded sufficient photosynthetic surface as an apical crown alone.

Thus we feel that the *Tempskya* plants appeared in life as indicated in the accompanying restoration (text-fig. 7). While, as noted at the outset, this is based on specimens that we have assigned to *Tempskya Wesselii*, the close anatomical sim-

ilarity of all of the described species of the genus suggests a generally comparable habit. We wish to note that the kind of foliage borne by these plants is *not known*. Although the leaves shown in the restoration are of the *Anemia* type this does not necessarily imply such a relationship. They have been used to indicate rather the approximate *size and distribution of the foliar organs*.

#### THE ROOTS

The roots of the Tempskyas have been described by previous investigators including Kidston and Gwynne-Vaughan ('11), Seward ('24), Read and Brown ('37), and Arnold ('45). A rather close similarity of the anatomy of these organs has been noted in the descriptions of the various species, and we are in agreement with these previous workers in that the roots seem to offer no recognizable specific characters. There are, however, certain points pertaining to their physiology that seem deserving of further consideration.

If it is kept in mind that the basal portion of the trunk of the mature plant is composed entirely of roots, and the trunk at any point is composed largely of them, it is evident that they played a more than ordinary role in the absorbing, conducting, and supporting functions of the plant. A detailed study of these roots presents some rather challenging problems, and the literature of comparable physiological set-ups in living plants is by no means a copious one.

The roots, like the stems, branch profusely and present in any section considerable variation in size, degree of maturity, and preservation. The stele is small and, like the stem, consists only of primary wood. In well-preserved specimens (fig. 13) the phloem and endodermis are clearly defined. It is not often possible to identify positively any tissue that may be called the pericycle. In fig. 13 a thin crushed row of cells, apparently the pericycle, may be noted between the endodermis and the large metaxylem tracheid in the upper-right portion of the figure. Very early in the maturation of the extra-stelar tissues a conspicuous fibrous middle cortex is developed. This tissue is extremely variable, at times extending to the endodermis (fig. 13), and its development is accomplished to a considerable extent by abundant radial cell divisions which result in a distinctive tangential alignment of the cells (fig. 19). Taken by the thousands it is evident that such structures would develop a trunk of great strength—certainly not a brittle one—yet the close organization of roots suggests one of considerable rigidity. Without this sclerotic cortex is a rather broad, thin-walled outer cortex (figs. 11, 17), in most cases largely decayed, the outer remnants of it forming a collapsed loop which encloses the tissues.

Although the roots in general average a little less than 1 mm. in diameter there is considerable range in size. Within an area of a square centimeter roots may be found that are less than .5 mm. and others nearly 2 mm. in diameter. The smallest of these (mature) roots may have a middle cortex consisting of only two rows of the very thick-walled fibrous cells, a row or two of large, thinner-walled outer cortex, and epidermis.

The nature of the outer cortex may have some bearing on an interpretation of



Text-fig. 7. A restoration showing the probable habit of *Tempukya*, based on specimens of *T. Weisellii*. Foliage has not been found attached to the trunk. For further explanation see text.

the compressed forms in which the trunks often occur. It is evident that many of the roots in a normal trunk, prior to removal of the plant from its place of growth or fossilization, were largely decayed. Just how much decay did take place immediately before silicification cannot be determined and certainly varied with different specimens. Certain parts of specimen T53 are exceptionally well preserved, and within a small area (fig. 14) some of the roots still retain the most delicate tissues while intimately associated with them are others with nothing but the sclerotic cortex intact. Some of the former are young roots in which little thickening of the sclerotic cells had occurred and they show root hairs as well; the latter may be interpreted as older roots that had been dead for some time.

In contrast to fig. 14, the majority of sections show very few roots in which the outer, large, thin-walled parenchymatous tissue is preserved. Here and there a root may be in almost perfect preservation, and less occasionally a considerable group will be well preserved. Others have the inner cortex and stele intact and in still others the stele is missing, as well as the remnants of the outer cortical loop. Many of them reached this stage through death and decay during the normal life of the plant. If, however, any appreciable number of roots were alive and active at a given time (as must have been the case) a considerable percentage of the area of the transverse section was composed of this large, thin-walled, readily decayable tissue. It would seem, then, that the general decay of this tissue immediately prior to fossilization would have allowed even a relatively slight lateral pressure of overlying sediments to have compressed the trunks.

A comparison of circular and variously flattened specimens has been made in order to determine the mechanism of flattening. However, no differences were ever observed that might point positively to mechanical crushing. It may also be noted that in specimen T53, where the preservation of immature roots is so perfect, there is no marked indication of distortion. If we should assume that a large percentage of the roots was actively functioning and with their outer cortex intact the roots would have been so closely compacted as to have been strongly angular in shape. Yet where an appreciable number of roots happen to be well preserved in a small area (fig. 14) this is not the case. There is some compaction due to crowded growth but it is not excessive. It may also be noted that in most areas the roots, or remains of roots, are so crowded that there could not have been room for them all to have existed with their outer cortical tissues at one time. The evidence therefore indicates that only a portion of the roots composing a trunk was active at a given time. In this connection it may be noted that Schoute found very few live roots of the many composing the dense matrix of the trunk of *Hemitelia crenulata* (see page 144).

In his treatment of *Tempskya Knowltoni*, Seward ('24, p. 494) makes the following pertinent remark: "The contrast between the large number of roots without any visible connexion with their mother-organs and the small number of which the origin is demonstrated is remarkable. Most of them must have come from stems or leaf-bases that are unrepresented in the specimen."

Unfortunately, this evidence does not indicate positively whether the flattening of the trunks was natural or the result of the pressure of overlying sediments prior to fossilization. In summary we are inclined to believe, however, that the flattened form is not natural for the following reasons:

1. In any trunk there was, in life, a mixture of live, active roots as well as others in various stages of decay.
2. This organization allowed sufficient "inter-root-stem" space for the reorganization of these elements when crushed by overlying sediments without presenting a recognizable microscopic effect.
3. No other observable characters correlate with the wide range in transverse shape.
4. Circular and flattened trunks alike in our collection display a symmetry that is radial with reference to the departure of leaf traces.
5. It seems doubtful that a single species would have existed in such a wide range of forms.

*Root hairs.*—In many of our specimens we have been able to observe well-preserved root hairs, some of which are very long, as shown in fig. 12. These root hairs are often found on the larger roots which, judging from their size and general maturity, would seem to indicate at some appreciable distance back from the apical meristem. That these hairs occur on the older portions of the roots is, moreover, adequately attested by the fact that they may be observed on numerous roots within a small area. There can be no doubt that these are either persistent root hairs produced at an earlier growth stage of the root or that they are simply developed from the epidermal cells throughout the life of the root. There is evidence to indicate both modes of origin. The root shown in fig. 11 represents one of average size and certainly mature. Numerous short root hairs may be noted. These are complete hairs, as evidenced by the uniformly rounded tips, and not simply broken remnants.

In describing living specimens of *Dicksonia fibrosa* in New Zealand (see page 145) Field ('90) refers to the absorbing capacity of the aerial roots. In *Tempskya* this function must have been of considerably greater importance than in most of the living ferns where the stem stelar system extends down to ground level. In the larger *Tempskya* trunks (10 to 12 inches in diameter) the stems had died away from the lower two feet, and possibly more, of the trunk. That portion of the trunk above this "root-stump" depended upon its water supply, then, either through the long slender roots reaching down from the stems or, more directly, through rain water absorbed from the apical and lateral surface of the trunk. There would seem to be little doubt that most of the minerals were taken up from the soil through the length of the trunk. However, the external surface of the trunk throughout must have been very absorbent and the trunk itself capable of retaining considerable moisture. The fact that deep within the trunk, roots are found with root hairs intact would seem to indicate that they functioned thus in drawing off this water reservoir.

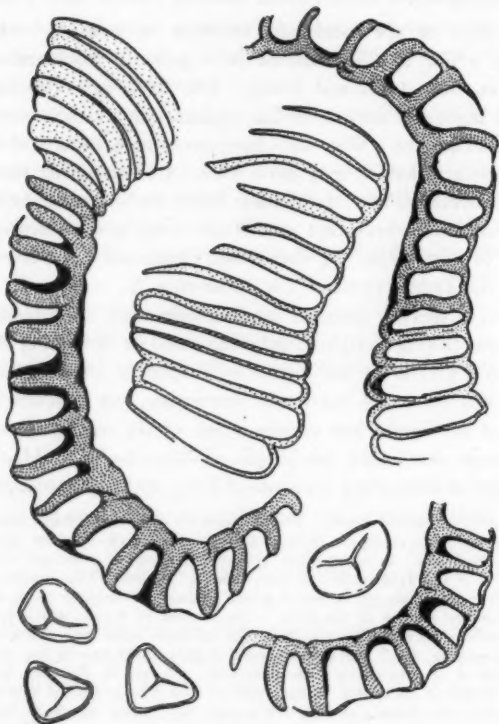
## COMPARISONS WITH OTHER PLANTS, LIVING AND FOSSIL

The morphology of the trunk of *Tempskya* represents a peak of structural evolution along a line that is manifest in a generally comparable fashion in a number of ferns, both fossil and living. The ferns have developed some very remarkable and ingenious devices in the organization of their primary tissues to bring about increased size. Why they have never been successful in the use of a cambium is a mystery that we may never know, yet their other modes of development have been successful to a considerable degree and are none the less interesting. We have no reason to believe that any of the other plants mentioned below are closely related to *Tempskya*, yet they seem significant in offering clues to the racial origin of the *Tempskya* trunk (or "false-stem").

Scattered rather sparsely through the literature there are references to a number of living ferns having upright trunks composed of branching stems which are held together to a greater or less degree by a mass of adventitious roots. Since some of these references are extremely interesting, yet obscure and mentioned only briefly, if at all, by previous writers, a few of the most pertinent ones will be considered in some detail. In his "Ferns of New Zealand" H. C. Field ('90) presents a number of interesting accounts of ferns with stems of upright habit:

"Rhizomes are of various kinds. The simplest form is that which grows 'erect' and produces its fronds in a crown or tuft at the top; in which case the plant is called a 'crowned' or 'tufted' one. In many ferns, this erect rhizome is prolonged above ground to a great height, as in tree ferns, and it is then called a 'caudex.' This caudex . . . is always clothed with fibrous rootlets by means of which moisture is imbibed from the atmosphere and helps the upward growth of the plant. The number of fronds which form the crown of the plant depends very much on the number of these aerial root fibres, our *Dicksonia fibrosa*, for instance, in which the actual caudex is only about two inches thick, while the fibres form a felted or interwoven mass, sometimes two feet in diameter, having often as many as forty fronds in its crown. Some caudices have a large conical base of root fibres; and in others this cone extends to the very top of the caudex, which is then of no great height, the whole mass being called a 'rootstock.' Sometimes an erect rhizome or caudex becomes flattened at the top and produces a great number of fronds, while at others it becomes divided into two or more branches, each of which produces a separate crown; and occasionally fresh crowns burst out of the side of a caudex. It is not quite certain how these originate. In some cases it appears to be the nature of the fern to divide itself in this fashion; in others, it seems as if young plants had grown on the face of a caudex; while in others it occurs by accident. I watched a case where a falling tree strained a supplejack tightly across the crown of a tree fern; with the result that the next spring the plant produced two crowns, one on each side of the supplejack, and thenceforth was forked. I have seen a *Cyathea dealbata* with five branched caudices and crowns, and an *Aspidium aculeatum* with seven, varying from three feet to five feet high." [pp. 11-12.]

From the point of view of comparison with *Tempskya* perhaps the most interesting of these extant New Zealand ferns is *Hemitelia Smithii*. This tree fern, which is known to attain a height of 20 to 30 feet, often divides at the tip into two or three branches. In 1886 Buchanan described a remarkable specimen from the slopes of Mount Cargill, near Dunedin. Buchanan's sketch of this tree-fern is reproduced in pl. 26. It is reported as being 16 feet high and with 16 branches and several buds. "The budding and branching may proceed from any part of the stem, and the specimen has several branches diverging in various directions, which again divide, as in dicotyledonous trees." According to the author's



Text-fig. 8. Spores and fragments of annuli found in a ground thin section made from specimen T16 (slide 1400). X 220.

brief description and figures, the branching is not dichotomous but rather "a branch is produced from a small bud, which pushes its way through the woody inner or true stem of the tree, and also the close fibrous outer covering." Shortly after the division of the single stele in the main trunk of this plant the resultant branches become separate as shown in the sketch. It thus differs from *Tempskya* in which the branches (except the extreme terminal portions) are permanently held together by the dense mass of roots. An interesting point of comparison, however, is that in *Hemitelia Smithii* the crowns of leaves on the respective branches are borne at different levels, thus differing from other tree ferns with "divided crowns," but not entirely unlike our concept of the mode of habit in *Tempskya*.

Another curious living fern is *Hemitelia crenulata* Mett., from the forests of Kandang Badak, Java, which was described by Schoute in 1906. It is a "tree fern"

(pl. 25) of considerable size, attaining a circumference of 201 cm. at 30 cm. above the ground. The basal two or three feet of the trunk consist of numerous branches enclosed in a dense matrix of roots, while above this the branches are free. Judging from Schoute's illustration of a specimen with a man standing beside it the plant attained a height of at least 12 to 15 feet. At ground level the trunk of *Hemitelia crenulata* contains but one stem while about 29 cm. above this it branches into three, while 28 cm. higher up seven branches are found. In the largest specimen reported, 33 branches are displayed which bear leaves in a crown as well as laterally. As may be noted, the branches grow horizontally out for a short distance and then ascend sharply.

The stem of *Todea barbara* Hook. f. seemingly presents an organization that is comparable to the above two ferns although we have been able to find but little information concerning the gross morphology of the trunk, most of the accounts dealing only with the cellular structure of individual stems, petioles, etc. Seward and Ford ('03) give the following account although it is not as pertinent to the present discussion as one might wish:

"The stem of *Todea barbara* may reach considerable dimensions, forming a short and thick mass covered with a dense felt of brown roots, which completely hide the main bifurcated axis. One of the numerous plants of *T. barbara* sent to Europe by the late Sir Ferd. von Mueller has been figured, in which the stem reaches a breadth of 2.5 metres, a height of 1.76 m., and a thickness of 1 m. J. Smith also described a specimen from the Victorian Alps of Australia measuring 5 ft. 8 in. in height, with a diameter of 7 ft. 9 in., and weighing 1 ton 3 cwt.; he adds that a plant was received at Kew in 1869 weighing 15 cwt. and bearing 30 crowns and 160 fronds. The stem of a *Todea barbara* in the Cambridge Botanic Garden measures 8 ft. in circumference and 3 ft. in height, with 14 distinct 'crowns'; at the present time the crowns bear 230 fronds, with an average length of 7 ft. 6 in." [p. 239.]

From the large number of crowns that these *Todea* plants bear there must be rather profuse branching of the stems composing a trunk. Unfortunately, we know very little about this, for, as Sahni ('28) notes: "The mode of formation of the false stem still needs elucidation."

Field's ('90) account of *Dicksonia fibrosa* is also worth quoting. He writes:

"The caudex seldom, if ever, attains the height of 25 ft., but is extremely stout in appearance owing to the mass of matted fibrous aerial roots which envelops the actual caudex and which is often 15 in. to 18 in. in diameter, and occasionally even more. Curiously enough, it is often larger in diameter above than below, particularly in plants not exceeding 6 ft. or so in height; which shows to how great an extent this fern absorbs nourishment from the atmosphere by means of its aerial roots."

This is the only case of obconical trunk shape, such as Seward reported for his single specimen of *Tempskya Knowltoni*, that we have come across in living ferns (other than in the very young stages). And, judging from Field's statement, it is not found in a completely mature plant. In view, then, of this data on living ferns and the fact that none of the hundreds of specimens of *Tempskya* from Idaho suggest such a trunk form it seems reasonably certain that Seward's specimen is either a very exceptional one or that it represents a fragment of a larger trunk.

The only fossil plant that seems to merit comparison with *Tempskya* is the Carboniferous zygopterid tree-fern from New South Wales described by Sahni

('28) as *Clepsydropsis australis*. Later, he ('32) gave reasons for its exclusion from that genus and proposed the name *Austroclepsis*. So far as we are aware its present valid name, then, is *Austroclepsis australis* (E. M. Osborn) Sahni.

It should be noted that there is no close genetic relationship between *A. australis* and the genus *Tempskya* for their individual stems and petioles have a strikingly divergent anatomy. Such resemblance as may be observed is only in the general habit of the trunks. In *A. australis* the petioles are large, almost equalling the stems in diameter; many petioles appear in a transverse section, indicating that they were long and the fronds persistent for some time; furthermore, the divisions of the stems are not nearly as profuse as in *Tempskya*. Thus the general appearance of *Austroclepsis* with its single crown of rather large fronds (Sahni, '32, text-fig. 14) must have been quite different from that of *Tempskya*. These two genera, widely separated in time and space as they were, possibly present in the gross organization of their trunks a similar evolutionary trend such as is exhibited in the above-mentioned living ferns, and it is a trend that probably took place independently in a number of different groups of ferns at different geologic times.

#### TAXONOMIC CONSIDERATIONS

As stated at the outset, our primary interest in this investigation was with the general habit, mode of growth, and physiology of the *Tempskyas*. A few points may be worth mentioning, however, in order to clarify our own taxonomic treatment as well as to offer suggestions that may be of use to future investigators. A careful identification of the specimens has, of course, been basic, and while we have assigned the name *Tempskya Wesselii* to most of our specimens other observers might find cause to split these into more than one species. Such "species" would be of very doubtful significance, and it seems certain that concepts pertaining to the life form and functions of the plants would stand unaltered.

Since the roots have presented no recognized taxonomic characters the identification of stump specimens can be made only to the genus. However, in view of their constant and uniform association with the trunk (disc) and tip specimens in the Wayan region there can be no doubt of their identity.

In view of the lack of evidence of natural affinities of the genus, Read and Brown ('37) created the family TEMPSKYACEAE, which constitutes the most expedient treatment. The only disappointment in our own investigation has been that such spores and sporangial fragments as were found in the trunks offer no positive help.

Prior to the work of Read and Brown eight species of *Tempskya* had been described: from Sussex, England; the basin of the Karaganda River in Russia; Bohemia; Maryland; and Montana. Many of these, because of their fragmentary nature and poor preservation, are certainly not worth further consideration and in their *Synopsis* Read and Brown have dealt with only two of them—*Tempskya rossica* Kidston & Gwynne-Vaughan from Russia, and *T. Knowltoni* Seward from Montana, and they have added two species, *Tempskya grandis* from Wyoming and

*T. minor* from Wyoming and Idaho.

More recently Arnold ('45) has described two more species: *T. wyomingensis* from "about twenty miles northeast of Greybull, Bighorn County, Wyoming, and *T. Wesselii* from Greenhorn, Oregon, and Great Falls, Montana.

Since it is perhaps most expedient to the present discussion we present the *Synopsis* of Read and Brown, to which we have added Arnold's two species in accordance with his concepts of their relationships.

#### SYNOPSIS\*

1. Individual stems of false stem large, with very short internodes as indicated by the numerous leaf bases present in transverse sections. Xylem exarch or possibly slightly immersed in some specimens. False stem chiefly radially symmetrical. Xylem ring containing much parenchyma.
  - A. Inner cortex a broad zone of parenchyma containing near its inner margin an irregular but continuous tract of sclerenchyma. Outer layer of "pith" a similar zone of parenchyma, containing sclerenchyma, especially in the vicinity of the nodes..... *Tempskya grandis*
  - B. Inner cortex a narrow zone of large-celled parenchyma. Presence of an inner sclerotic layer not recorded..... *Tempskya rossica*
  - C. Inner cortex with two bands of stone cells. Smaller stems and longer internodes than the above two..... *Tempskya Wesselii*
  - D. Individual stems large (6-8 mm. in diameter), very close to *T. grandis*, differing chiefly in having a double layer of stone cells; internodes and stems larger than in *T. Wesselii*..... *Tempskya wyomingensis*.
2. Individual stems of false stem small, internodes of such length as to permit only a little overlapping (2-3) of leaf bases. Xylem exarch. False stem dorsiventral. Xylem ring containing little, if any, parenchyma.
  - A. Xylem very compact; protoxylem commonly segregated into definite groups. Inner cortex broad, parenchymatous. Petioles common in false stems, indicating persistence of leaves; xylem arch, fairly flat. Stems averaging larger than those in the next group..... *Tempskya minor*
  - B. Xylem compact but with parenchyma in places interspersed with the tracheids. Inner cortex usually narrow, parenchymatous. Petioles rare in false stem; xylem arch, rounded..... *Tempskya Knowltoni*

\* From: Read, C. B. and R. W. Brown: American Cretaceous ferns of the genus *Tempskya*. U. S. Geol. Survey Prof. Paper 186-F, p. 119. 1937, except parts C and D under 1, which have been abstracted from: Arnold, C. A.: Silicified plant remains from the Mesozoic and Tertiary of western North America. Mich. Acad. Sci., Arts, and Letters 30:24-33.

Read and Brown have considered the gross organization of the trunks, that is whether radially or dorsiventrally symmetrical, of importance, while Arnold places considerable weight on the structure of the cortex in the delimitation of species.

In almost all cases where it is certain that we are dealing with complete transverse sections the symmetry of the trunks is essentially radial. In order to present some quantitative evidence of this we have taken a representative sampling of specimens displaying different shapes and noted the direction of departure of the petioles (Table III). These show quite clearly that the departure of the petioles is usually toward the nearest periphery of the trunk, as shown in text-figs. 2 and 5. It is not surprising that an occasional stem should bear its leaves toward the center rather than the periphery of the trunk but this does not necessarily point toward

TABLE III

COMPILATION, FROM A REPRESENTATIVE SELECTION OF SPECIMENS, OF STEMS, CONTRIBUTING TO RADIAL OR DORSIVENTRAL SYMMETRY OF THE TRUNKS, THE FORMER BEING STEMS IN WHICH THE PETIOLES PASS TOWARD THE NEAREST PERIPHERY OF THE TRUNK, THE LATTER THOSE WHICH ARE IRREGULAR IN THIS RESPECT

Specimen and peel number	Shape and dimensions in transverse section (inches)*	Total number of stems	Ratio of dorsiventral to radially symmetrical stems	Percentage of stems contributing to radial symmetry
T205, B1	E $3 \times 2$	57	1:50	98
T2, T5	E $5\frac{3}{4} \times 1\frac{1}{2}$	50	3:38	95
T47, T19	E $5\frac{3}{4} \times 3\frac{1}{2}$	134	0:114	100
T3, T5	E $3\frac{1}{2} \times 2\frac{1}{2}$	68	5:58	92
T90, AT8	E $3\frac{1}{2} \times 2\frac{1}{2}$	67	3:54	95
T51, GB T1	T $4 \times 3$	74	5:56	92
T201, A1	E $2\frac{3}{4} \times 2$	53	3:47	94
T202, B1	T $3 \times 1\frac{1}{2}$	27	2:23	92
T5, T2	C $2\frac{1}{2}$	20	2:18	90
T4, T1	E $3\frac{1}{2} \times 2\frac{3}{4}$	70	1:55	98
T17, T3	C $2\frac{3}{4}$	52	7:47	87
T53, T3	E $6\frac{1}{4} \times 2\frac{1}{2}$	96	1:81	99
T45, T5	E $3\frac{3}{4} \times 3$	60	6:48	89
T42, T7	E $4 \times 3\frac{1}{2}$	68	5:58	92
T33, T7	E $7\frac{3}{4} \times 4$	158	3:122	98

\* E, elliptical in transverse section; T, triangular; C, circular. The stems in the central third (diameter) of the trunks have been omitted since these are more variable in the direction of departure of the petioles and represent for the most part the terminal stems of the trunk.

asymmetry of the trunk as a whole. Since the stems probably projected out a short distance beyond the trunk proper it is quite conceivable that they could have given off leaves on the inner as well as the outer side.

In only one of our specimens is there a tendency for the petioles to pass predominantly in one direction. This is a small specimen, or quite possibly a portion of a larger one. It must be admitted that while our own observations are based on a large number and variety of specimens their geographical distribution is not great. We feel inclined to predict, however, that when comparable collections are gathered from other regions and when it is certain that the individual specimens are complete in transverse section, they will reveal radially symmetrical trunks.

With respect to the anatomy of the cortex, we have noted under the "Techniques" section differences that may be encountered in a study of identical stems of a trunk using peel preparations *vs.* ground thin sections. Also important is the variation in this character (particularly the apparent presence or absence of the stone cell band on the inside and outside of the inner cortex) that may show up in consecutive peels taken from the same specimen. With the proper etching time the sclerotic bands stand out in striking contrast to the parenchymatous tissue; but where the time is too little or too great the contrast may be much less apparent, or even barely discernible.

These differences are pointed out as neither an indictment against the methods themselves or the results of previous workers but to show that there are two points of the utmost importance in studying the genus *Tempskya*:

1. Specimens displaying complete or nearly complete transverse sections of the trunk are absolutely essential to taxonomic and morphologic studies.
2. Great caution must be exercised in delimiting species with reference to the way in which sections are prepared.

We feel that our own investigation has shown the probable lack of taxonomic significance in the gross symmetry of the trunks as used in the preceding synopsis. Furthermore, in view of the rather close gradation of the other characters that have been used to delimit species, as well as the fact that some have been based on rather scanty material, there is considerable doubt whether *Tempskya minor*, *T. Knowltoni*, *T. Wesseli*, and *T. wyomingensis* represent distinct species. We do not wish to carry this taxonomic problem further but as our knowledge of *Tempskya* grows it is likely that rather extensive revisions will be necessary.

*Spores and sporangia.*—In 1895 Boodle described some spores that he found in a specimen of *Tempskya* identified as *T. Schimper*, collected near Brightstone in the Isle of Wight. These are  $65\ \mu$  in diameter and "spherical or oval to bluntly tetrahedral," with a spore wall conspicuously sculptured with long bars. He noted a close comparison of these spores with those of the living *Anemia elegans* (Schizaeaceae), although he also points out that *Ceratopteris thalictroides* (Parkeriaceae) has spores with a similar sculpturing.

Seward found in his specimen of *T. Knowltoni* structures which appear to be the annuli of a Schizaeaceous fern, and probably belong to the genus *Anemia*. It is largely on account of these reproductive organs that *Tempskya* has been thought to be of Schizaeaceous affinities.

The only contribution that we have been able to make in this direction perhaps confuses the picture more than it helps to clarify it. Ground thin sections of two of our specimens (T16 and T3) contain considerable numbers of spores and fragments of the annuli of fern sporangia. The spores occur as isolated individuals, as well as aggregations of about 100 to 200, and in all cases the exine appears quite smooth. They are mostly collapsed, but a few appear triangular to slightly elongate (text-fig. 10 and fig. 23), these averaging about  $50 \times 40\ \mu$ . The spore shown in fig. 23 measures  $51 \times 36\ \mu$ .

The lack of any sculpturing of the spore wall and the occurrence of spores in large masses might lead one to infer that they are simply immature. However, since the exine is smooth in all of them, and an appreciable number is scattered about as individuals, it is probable that this is a mature character. For whatever the comparisons are worth it may be pointed out that there is a general lack of surface ornamentation throughout the genus *Gleichenia* (Gleicheniaceae), while *Thyrsopteris elegans* (Dicksoniaceae) has spores that are likewise smooth-walled (Knox, '39) and compare closely with our fossils.

Associated with these spores are some annulus fragments (text-fig. 10). Speculations on these fragments can lead to no definite conclusions although it seems clear that they are not Schizaeaceous, nor is it likely that they represent the

Osmundaceae or Gleicheniaceae. A much closer comparison seems to be afforded by the modern Polypodiaceae or possibly the Cyatheaceae-Dicksoniaceae.

We have chosen to refer our specimens to *T. Wesselii* Arnold because they compare most closely with the published description of that species. For those who may be especially interested in *Tempskya*, as well as for the purposes of record, we have compiled short descriptions of a representative selection of specimens of *T. Wesselii* in our own collections, pointing out especially distinctive characters that the respective specimens present:

*Specimen T33.*—A disc specimen measuring nearly  $8 \times 4\frac{1}{2}$  inches in transverse section and 6 inches long. This seems to be representative of the larger, flattened trunks. Approximately 160 stems are found in a single transverse section, of which about 74 are shown in various stages of branching. The individual stems average 3.5 mm. in diameter, most of them being fairly close to this figure, although a maximum variation of from 1.5 mm. to 5 mm. in diameter may be found. The steles in the peripheral inch of the trunk are, for the most part, appreciably better preserved than those deeper within. Such differentiation of preservation is not as noticeable in the smaller specimens.

*Specimen T2.*—A much-flattened tip specimen (fig. 26 and text-fig. 3) approximately  $6\frac{1}{2} \times 1\frac{1}{2}$  inches in diameter and  $2\frac{3}{4}$  inches long. Of the 57 stems shown in transverse section 18 are branching. The stems average 3.5 mm. in diameter, with a maximum variation of 2 to 4 mm. The preservation is uniform throughout the specimen, as might be expected in a small trunk tip.

*Specimen T53.*—A flattened, nearly oblong-shaped disc measuring  $6\frac{1}{2} \times 2\frac{1}{2}$  inches in transverse section and  $2\frac{1}{2}$  inches long. This is unusual only in the mode of preservation, the smoothed surface (and peels) presenting a characteristic blotched appearance due to the irregular quality of preservation.

*Specimen T47.*—A somewhat flattened tip specimen 9 inches long, in which a transverse section 5 inches from the top measures  $6 \times 3\frac{1}{2}$  inches. Of the 134 stems in one transverse section, 45 are shown in various stages of dichotomizing. Each stem is giving off petioles toward the nearest point on the periphery of the trunk, thus producing perfect radial symmetry. Stems in the central part of the trunk are shown in perfect transverse section in any peel preparation, whereas those toward the periphery are shown, in the same peel, in somewhat oblique section, indicating that the stems at the edge of the root mass bend slightly outward while those in the center of the trunk keep a more or less vertical course.

*Specimen T216.*—A disc specimen 13 inches long which is somewhat triangular in transverse section. The transverse section at the bottom of the specimen measures  $6\frac{3}{4} \times 5\frac{1}{4}$  inches, while at the top it measures  $6 \times 4\frac{1}{2}$  inches. Several hundred stems are present in a single transverse section, the radial arrangement of which is apparent.

*Specimen T27.*—A very much flattened, small disc specimen from Mr. Thomas's collection, about  $4\frac{1}{2}$  inches long and measuring about  $3\frac{1}{2} \times \frac{7}{8}$  inches

in transverse section at the top. At that point only eight stems are present in the transverse section, and all but one of these are in some stage of branching. The stems average  $2\frac{1}{2}$  mm. in diameter, and are well preserved.

*Specimen T90*.—A small, very well-preserved disc specimen, approximately  $3\frac{1}{2} \times 2\frac{1}{2}$  inches in transverse section and about  $2\frac{3}{4}$  inches long. Serial sections were made of this specimen, and the branching of three of the stems was followed for a distance of  $4\frac{1}{2}$  cm., as illustrated in text-fig. 4. Approximately 55 stems are found in a single transverse section, of which 22 are in various stages of dichotomizing. Individual stems vary from  $1\frac{1}{2}$  to 4 mm. in diameter, with most stems measuring 3 mm. in diameter. Preservation of the stems varies somewhat, although in no apparent set pattern.

*Specimen T229*.—This is a rather large disc specimen (fig. 9) and is especially unique in that it is crescent-shaped in transverse section, the latter measuring nearly  $13 \times 6$  inches. Two discs, totaling about 12 inches long, were found, one of which is in Mr. Thomas's collection and one in ours under the above number. Most of the stems are in a rather advanced state of decay, due primarily to the fact that the specimen came from toward the lower part of a trunk as is indicated by the fact that many of the stems are invaded by numerous roots.

#### ASSOCIATED PLANT REMAINS

In his description of *Tempskya wyomingensis* Arnold ('45) has mentioned "occasional fragments of the trunks of *Cycadeoidea*, which resemble those from the Freezeout Mountain locality north of Medicine Bow" associated with the fern material in the valley of Beaver Creek, Bighorn County, Wyoming. Aside from that reference, nothing has been reported so far as we are aware concerning the plants with which *Tempskya* may have been associated in life.

We have been fortunate in finding in section 27 (Lanes Creek quadrangle, see text-fig. 1) rather abundant fragments of a dicotyledonous wood, a coniferous wood, and a portion of the trunk of a *Cycadeoidea*. Although these plant remains were found only in the one locality they serve to give us some concept of the ecology of the Tempskyas.

Judging from the very faintly defined annual rings of the fossil woods seasonal climatic fluctuations probably were not great, and the presence of the cycad, as well as the cycad and dinosaur fragments reported by Arnold, would suggest a generally warm climate. If the growth requirements of *Tempskya* were at all comparable with those of modern tree ferns the climate must have been a tropical one.

In trying to arrive at a tentative comparison with modern floras and climates we have drawn on the extensive field experience of Mr. Paul H. Allen, the Garden's tropical plant collector in Central America. The following is, we feel, of some comparative significance:

"The only modern conifers associated with tree ferns in the American tropics would be species of *Podocarpus*, usually found in the highlands between 3000 and 7000 feet. Slender

species of tree ferns occur as isolated specimens in heavy rain forest from sea level to 6000 or 7000 feet, being replaced by stouter, handsome species at higher elevations. Greatest concentrations of individuals, however, are found in open, unshaded locations having ample moisture, such as banks of small streams in pastures (vicinity of Villavicencio, Meta, Colombia), abandoned fields growing up to second growth (highlands of Chiriquí—4,000 to 6,000 ft.), moist sunny canyons in dry grassland (badlands of lowland Coclé), or sunny moist roadside banks in forested areas (vicinity of Puerto Pilon, Canal Zone), or National Highway near Remedios, Chiriquí Province, Panama. No true cycads occur in the Americas in close association with tree ferns in modern times, but I have seen species of *Zamia* growing in the same area with them about Madden Lake in the Zone, and in patches of forest along the Rio Ariari in Colombia.

"Summarizing, tree ferns grow in greatest concentration in relatively open, sunny situations, and there is, so far as I know, nothing that could be described as a typical tree-fern association of plants. Thus, while tree ferns might by pure coincidence be found with *Podocarpus* or *Zamia*, they might just as often, or rather more often, be found with other things."<sup>5</sup>

In a consideration of the climate of this region during middle Upper Cretaceous times it is pertinent to recall the presence of *Anemia Fremonti* and *Gleichenites coloradensis* in the Frontier formation of southwestern Wyoming. These are fern species with undoubted relationships to the modern genera *Anemia* and *Gleichenia*, both of which are tropical to warm sub-tropical in their present distribution. Although the fossils were found south of Kemmerer, Wyoming, the Frontier formation extends north to a point less than 25 miles from Wayan, and the actual distance to the Kemmerer locality is less than 100 miles.

We do not know what the exact correlation is between the Frontier and Wayan formations; the latter may lie slightly below the former (Read and Brown, '37, pl. 27). Yet, it is safe to assume that the two are not far apart. Thus since these two ferns of tropical affinities were contemporaneous and inhabited the same area, or very nearly so, as the Wayan *Tempskya* flora, we are inclined to consider this southeastern corner of Idaho and adjoining Wyoming as being clothed in tropical forests covering undulating hills of altitudes up to possibly 4000–7000 feet, and favored by a climate that was uniformly moist and warm throughout the year. The more exact floristics of the "*Tempskya* forests" must remain in doubt, although the Colombia and Canal Zone habitats suggested by Mr. Allen seem to present a very likely comparison.

*Tempskya* as animal food.—It does not seem entirely improbable that the *Tempskya*s constituted an important dietary item for certain larger animals of the time, such as the Cretaceous herbivorous dinosaurs. Diversified as the dinosaurs were in form and environmental adaptations, some of them almost certainly must have occupied the habitat of these ferns. The association of their bone fragments (see p. 124) with *Tempskya*s adds support to this belief.

If our concept of the habit of *Tempskya* is correct it presented an ideal browsing plant. With the foliage distributed over a considerable portion of the trunk, rather than in merely a crown at the top, the leaves were available to herbivores both small and large. Each plant bore a considerable quantity of foliage even though the individual leaves were small. From the abundance and wide distribution of the *Tempskya*s in certain regions it would seem possible that they may have been of considerable importance as animal food.

<sup>5</sup>From a letter received from Paul H. Allen, Gamboa, Canal Zone, May 7, 1946.

## BENNETTITALES

*Cycadeoidea* sp.—In the summer of 1946 Mr. Thomas found two cycad specimens in section 27 (see text-fig. 1). One of these is a very small fragment while the other, described here briefly, is a portion of what was apparently a columnar trunk and measures 7 inches long and 9 x 7.5 inches in diameter. Its owner has preferred that the specimen remain intact, and since it is rather poorly preserved and with no strobili in evidence it is doubtful whether sectioning would reveal significant evidence. In the transverse section the leaf base zone is about 1.5 inches wide, while the entire central portion of the trunk is largely replaced by silica. At one point a small fragment of the wood is intact and measures slightly less than 2 cm. thick. Like the *Tempskya* specimens, this cycad trunk fragment shows no evidence of prolonged water transport; thus its chief interest lies in the probable association of these plants with the ferns in the Cretaceous landscape of the Wayan region.

## CONIFERALES

*Cupressinoxylon* sp.—In transverse section (fig. 31) this wood presents two conspicuous features: (1), the annual rings are not sharply defined, there being very few "late summer" tracheids marking that year's growth from the first cells of the following year; and (2), resinous parenchyma is profusely scattered through the wood.

In tangential view (fig. 32) the rays may be seen to vary from 2 to 40 cells high and predominantly uniseriate with an occasional biseriate one. There is no evidence of pitting in the tangential walls of the tracheids. The preservation is not sufficiently good to allow observation of the finer diagnostic details in radial section. Tracheidal pitting, however, is of the abietinean type and, for the most, part uniseriate, while the rays appear to be uniformly parenchymatous, there being no evidence of ray tracheids.

## DICOTYLEDONEAE\*

## SOME NOTES ON METHODS

The problems of studying effectively silicified trunks that range up to 16 inches in diameter need hardly be emphasized. Furthermore, although the abundance in which the fossils were found during the second and third trips to Wayan was most encouraging, one could not help but wonder whether a sufficiently comprehensive study could be completed within a reasonable period. In general, we have selected only the more complete and apparently better-preserved specimens for microscopic study. Some sort of critical concentration of material was obviously necessary at the outset, and while specimens of importance, possibly representing new species of significant morphological features, may have escaped our attention we do not feel that the number is high.

In preparing study material recourse has been made to the ground-section and the peel methods. Specimens up to about 5 inches in diameter were cut in our own laboratory, while the larger ones have been cut by the Pickel Stone Company

\* As it has not been possible to prepare a discussion of the associated dicotyledonous wood without seriously delaying publication this will appear at a later date.

of St. Louis. Such firms, having equipment for cutting and polishing large monument stones, may prove of considerable aid in paleobotanical work, and the cost is not excessive.

In all cases we have first made peel preparations of the complete transverse section. There is almost no limit to the area of a section made with this method provided adequate cutting and grinding equipment is available. These peel preparations proved invaluable in studying the gross organization of the trunks as well as detailed cellular anatomy in the better-preserved material. A few other points with reference to the peel technique seem worth recording. The quality of preservation in different portions of a peel taken from a transverse section often varies considerably. Generally, in the larger trunks, the central portion is not as well preserved as the more peripheral parts. This would be expected in accordance with our concept of the mode of growth of the trunks. In some, mineralization apparently was not uniform throughout the trunk.

Especially important is the fact that the degree of etching prior to pouring the peel solution had to be especially precise in this material, far more so than in any other petrifications that we have studied. As typical of this we may point out the differences observed in the parenchymatous inner cortex of the stems where that tissue is bounded on the inside by sclerotic nests and often on the outside by a thin sclerotic band. With the proper etching time these sclerotic tissues stand out in striking fashion. However, when the time was too long, very dark peel resulted, or when the time was too short, the peels were so light that such tissues could hardly be distinguished at all. In this respect Arnold ('45, pp. 27-28) reports that in *T. Wesselii*, "A peculiarity in the chemical make-up of these stone cells is that in sections prepared by the 'peel' method they are not recognizable, which indicates that they are soluble in the hydrofluoric acid used in the etching process." While this may be true in some specimens it has been our experience that the peels can be made to show the sclerotic tissues just as well as ground sections although some experimenting must be done with the etching time to have it perform to the best advantage.

Ground sections have been prepared from the better-preserved specimens. These have revealed certain of the more minute cellular details, especially in the root structure, in a more satisfactory manner than peels. Most of the best *Tempskya* specimens are black, indicating the presence of a large percentage of the original organic matter. These necessarily must be ground very thin to render sufficient transparency. We have found that the thermoplastic cement known as "Lakeside No. 70," prepared by the Lakeside Chemical Company in Chicago, is far superior to balsam as an adhesive. It is convenient and economical to use, sticks very tenaciously to glass, and does not, as is often the case with balsam, present the difficulty of being too soft or too brittle.

## SUMMARY

1. Fossil plants referable to the genus *Tempskya* have been known for over a century from European localities including England, Bohemia, and Russia. More recently a number of species have been described from northwestern United States.

2. The *Tempskya* trunk (false-stem) is composed of many branching siphonostelic stems held together by a dense mass of small, diarch, branching, sclerotic roots. Over 200 stems have been found composing the trunk of some specimens.

3. The specimens described in this report were collected in southeastern Idaho chiefly in the vicinity of Wayan, and have weathered out of the Upper Cretaceous Wayan formation. Other specimens have been obtained from a locality east of Ammon, Idaho.

4. The largest specimen measures 16 inches in diameter although fragments of others suggest a somewhat greater maximum size. It is calculated that a trunk 10 inches in diameter attained a height of approximately 12 feet, while the largest ones may have reached heights of 19 or 20 feet. The trunks were erect or very nearly so.

5. In transverse section the trunks vary from circular to strongly flattened, although in nearly all cases the departure of the petioles indicates radial symmetry. It seems very likely that the flattening has been caused by crushing prior to silicification.

6. In larger trunks the basal portion consists of roots only. As the stems in this region decayed their place was taken by roots.

7. Lateral and longitudinal growth took place by frequent branching of the individual stems, one of the two usually soon ceasing to grow. The leaves were small judging from the relatively minute size of the petioles, although they were very numerous on the trunk as a whole. The leaves were given off in two rows from each stem and probably were borne over two-thirds or more of the length of the trunk instead of only in a crown as in modern tree ferns and cycads.

8. A detailed consideration is given of the organization and apparent physiology of the roots.

9. Comparisons are drawn between certain living species of *Hemitelia* and *Todea* as well as a Carboniferous *Clepsydropsis*. The highly peculiar anatomical organization of *Tempskya* does not compare closely with that of any other fossil or living plant although those mentioned above, among others, seem to present a similar "growth tendency" which apparently originated independently in a number of fern groups.

10. A synopsis (taken from the works of Read and Brown, and Arnold) is given for the better-known American species, and all of the specimens on which this paper is based are referred to *Tempskya Wessellii* Arnold. It seems clear that all of the American species were closely related and very similar in general habit.

11. Spores and sporangial annuli have been found in two specimens.

12. Associated with the *Tempskya* trunks in the Wayan district are fragments of coniferous and dicot woods, and a specimen of a cycadeoid.

## ACKNOWLEDGMENTS

I am sure that my friends in Idaho have wondered, during the years that have elapsed, about the little there was to show in the way of published results, and this paper is brought out with a feeling of deep gratitude for their cooperation and patience and the hope that some measure of worth and satisfaction has rewarded their efforts.

For his generosity and ever-ready willingness to guide me along the little-known paths of his state I am very grateful to William A. Peters of Jerome, Idaho. Sincere thanks are also due Ralph and Blanche Peters. A very large share of the credit for whatever contributions may have been made to the story of the *Tempskya*s is due Henry Thomas, of whom appreciation has been recorded elsewhere in the text. For the specimens obtained from the Ammon locality thanks are due Mr. E. Manion, of Firth. Last but not least it is a pleasure to acknowledge the kind hospitality of the ranchers of Wayan whose cooperation in many ways has added immeasurably to the success of the field work.

We are also indebted to Dr. C. A. Arnold for kindly presenting specimens of *T. Wesseli* and *T. wyomingensis* from his own collections.

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## EXPLANATION OF PLATE

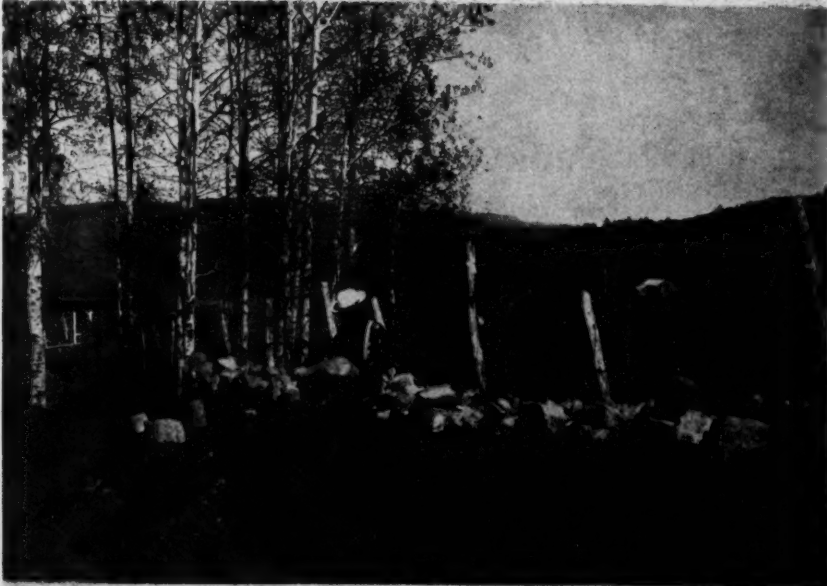
## PLATE 15

Fig. 1. A representative view of the hills southeast of Wayan, Idaho. Numerous specimens were found along the slope in the center, and on the left slope of the hill in the background.

Fig. 2. Mr. Henry Thomas and a portion of his *Tempskya* collection. Wayan, Idaho.



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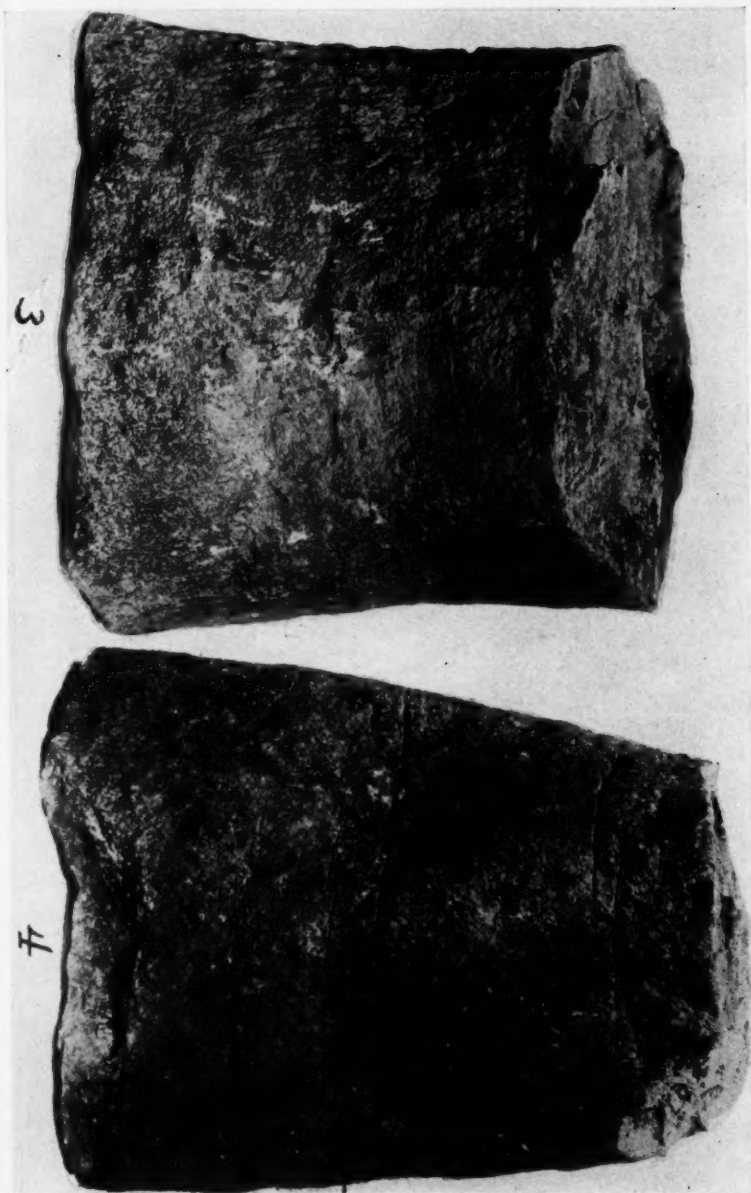
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## EXPLANATION OF PLATE

## PLATE 16

Fig. 3. A specimen of the basal end of a trunk showing roots only; basal circumference of specimen 36 inches, upper circumference 32 inches. This specimen differs from most in that the under side of the base is uniformly hollowed, forming a large single cavity with a maximum depth of about 1 inch in the center. Thomas collection.

Fig. 4. A portion of a trunk showing somewhat more rapid tapering than is usual in one of this length; basal circumference 29 inches, upper circumference 24 inches, length 13 inches. Thomas collection.



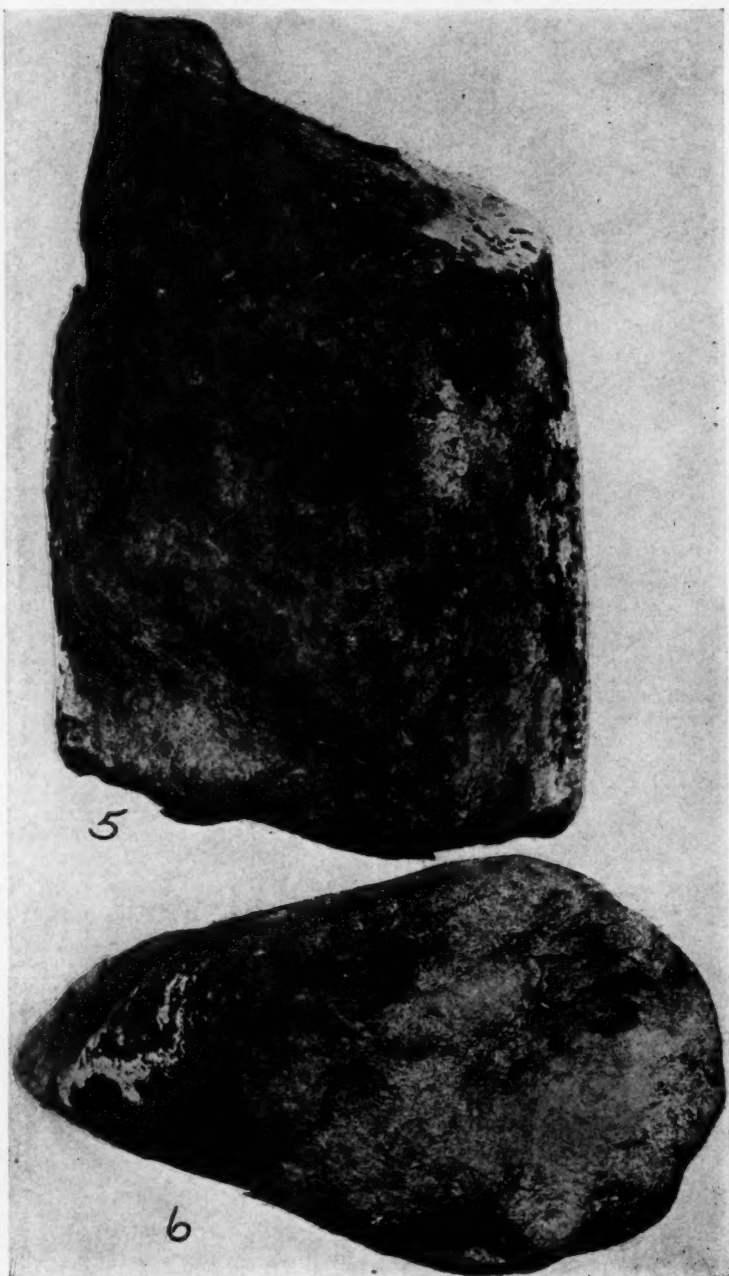
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## EXPLANATION OF PLATE

## PLATE 17

Fig. 5. A basal portion of a trunk nearly circular at the bottom and somewhat flattened above.

Fig. 6. A view of the under side of the base of the same. Henry Shaw School of Botany collection, T83.



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## EXPLANATION OF PLATE

## PLATE 18

Fig. 7. A typical specimen of the base of a trunk, composed only of roots; circumference at upper end 23 inches. Thomas collection.

Fig. 8. One of the two specimens in the entire Wayan collections which shows any appreciable curvature; lower circumference 25 inches, upper circumference 22 inches. In transverse view this specimen is somewhat flattened, the diameters of the upper end being  $4\frac{1}{4}$  x  $3\frac{1}{4}$  inches respectively. Thomas collection.



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## EXPLANATION OF PLATE

## PLATE 19

Trunk (disc) specimens of *Tempskya* showing the flattened form in which many are found.

Fig. 9. A rather large and unique specimen in that it is crescent-shaped in transverse view. This is a short disc, the major and minor diameters measuring 13 x 6.5 inches. Henry Shaw School of Botany collection, T229.

Fig. 10. End view of three disc specimens from the Thomas collection showing varying degrees of flatness in transverse section. The specimen at the left is not a complete disc, the side at the bottom of the photo representing a broken surface. Dimensions of the (transverse) ends shown in the photo are: left, circumference 17 inches, diameters 7 x 2 inches; middle, circumference 17½ inches, diameters 6¾ x 3¼ inches; right, circumference 17 inches, diameters 7 x 3 inches.



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## EXPLANATION OF PLATE

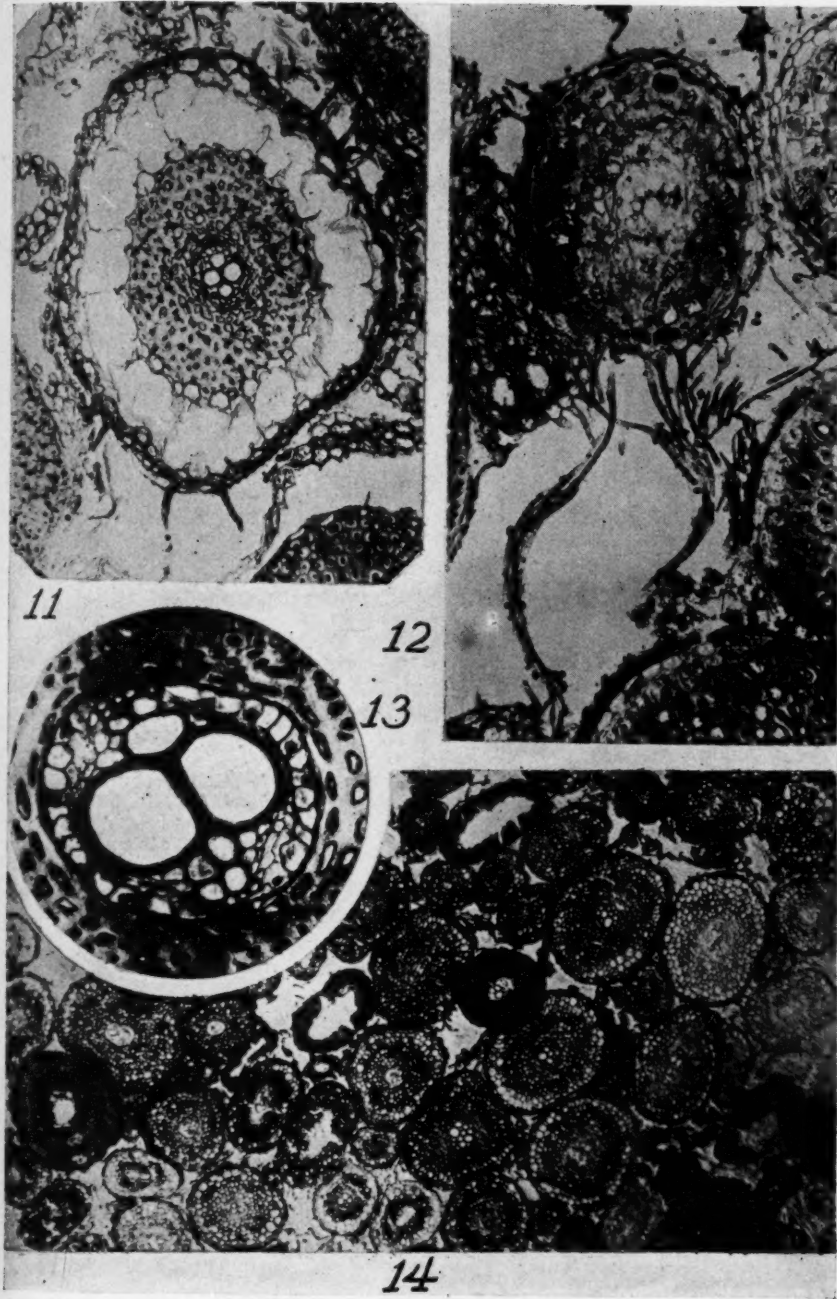
## PLATE 20

Fig. 11. An older root showing young root hairs produced on the "loop" of the outer cortex. From slide 1406, x 70.

Fig. 12. Root-hair development of smaller root. From slide 1406, x 80.

Fig. 13. Stellar structure of a root in which xylem, phloem, pericycle and endodermis are distinguishable. From slide 1411, x 175. Detailed description in text.

Fig. 14. A portion of the root mass showing various stages of preservation in adjoining roots, some perfectly preserved, others with merely the circle of sclerotic middle cortex remaining, thus indicating that roots were not all alive but in various stages of decay at the time of fossilization. From peel T53-4, x 17.



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## EXPLANATION OF PLATE

## PLATE 21

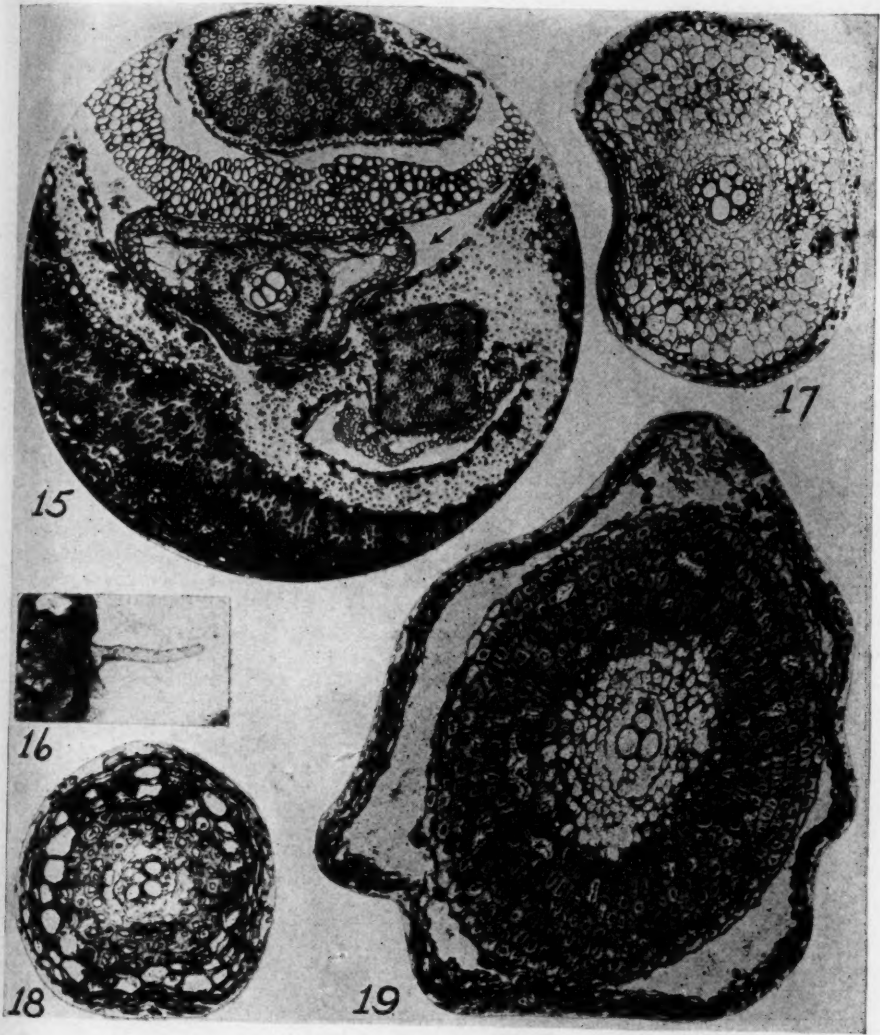
Fig. 15. A small root which has penetrated a stem and is bearing a root hair, indicated by arrow. From slide 1409, x 48.

Fig. 16. Enlarged view of the root hair in fig. 15, x 280.

Fig. 17. A young root with just the beginnings of a sclerotic middle cortex, and the delicate outer cortex complete. From peel T53-2, x 50.

Fig. 18. A very small, but older root, as indicated by the sclerotic middle cortex. From peel T17-11, x 80.

Fig. 19. An older root showing the tangential rows of sclerotic cortical cells and the "loop" produced by the disappearance of the delicate outer cortical cells. From peel T17-8, x 53.



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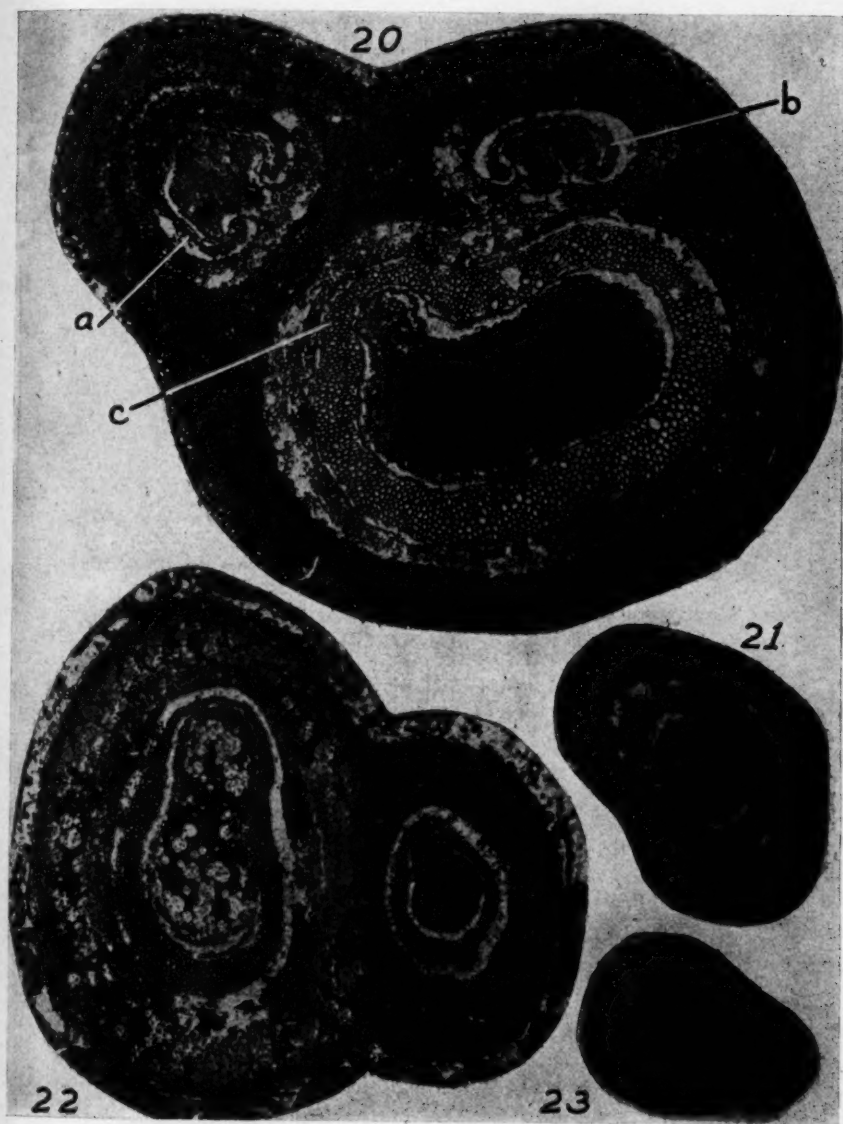
## EXPLANATION OF PLATE

## PLATE 22

Figs. 20 and 21. Two stems found in peel T17-7, illustrating the variation in stelar size in a single trunk section. The large stem shown in fig. 20 bears two leaf traces, *a* and *b*. A third one (*c*) may be seen to be nearly ready to depart from the stem stele. Both figures x 20.

Fig. 22. A stem showing unequal dichotomy, from peel T33-2, x 20.

Fig. 23. One of the spores found down among leaves and stems in specimen T16. From slide 1400, x 500.



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## EXPLANATION OF PLATE

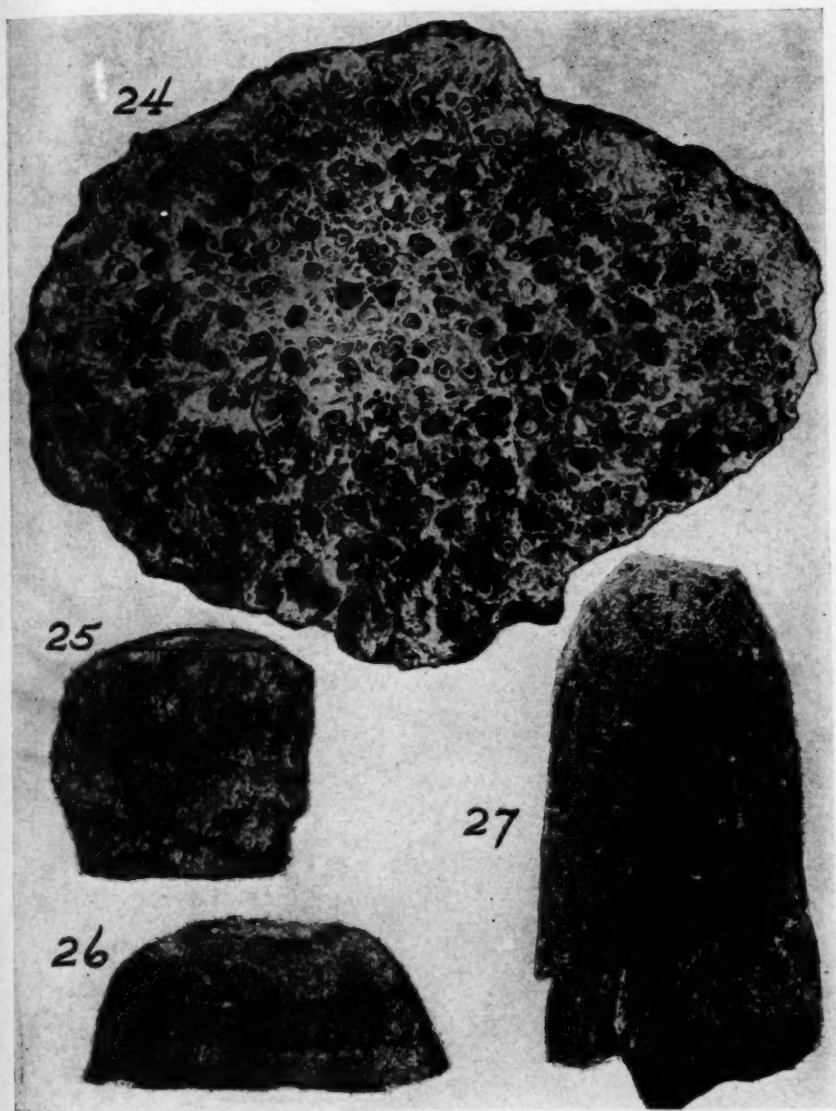
## PLATE 23

Fig. 24. A specimen from the Thomas collection, with 192 stems present in its area of  $5\frac{1}{2} \times 4$  inches. The specimen was from  $\frac{7}{8}$  to  $1\frac{1}{2}$  inches thick.

Fig. 25. A much flattened disc specimen (T27) which measures  $3\frac{1}{2} \times \frac{7}{8}$  inches in transverse section at the top, and  $4\frac{1}{2}$  inches in length.

Fig. 26. A flattened tip specimen (T2) which measures  $6\frac{1}{2} \times 1\frac{1}{2}$  inches in transverse section at the base and  $2\frac{1}{4}$  inches in length.

Fig. 27. A tip specimen (T230) which measures  $6 \times 3\frac{1}{2}$  inches at the base and 12 inches in length.

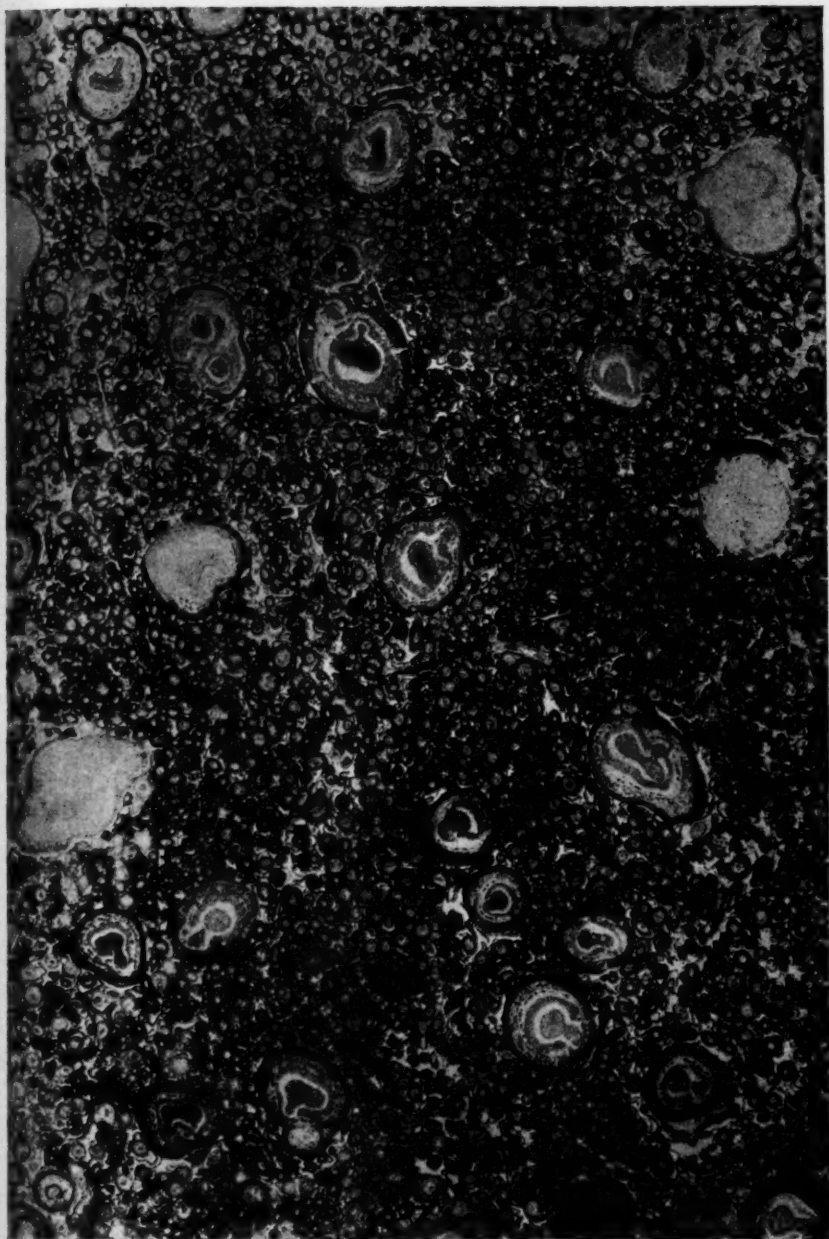


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## EXPLANATION OF PLATE

## PLATE 24

Fig. 28. Transverse view of part of a *Tempskya* trunk showing about 26 stems.  
From peel T51, C, T13, x nearly 5.



## EXPLANATION OF PLATE

## PLATE 25

Fig. 29. A partially dissected specimen of the modern *Hemitelia crenulata*. From: Schoute, J. C., Eine neue Art der Stammesbildung im Pflanzenreich (*Hemitelia crenulata* Mett.). Ann. Jard. Bot. Buitenzorg, pl. 19, fig. a. 1906.



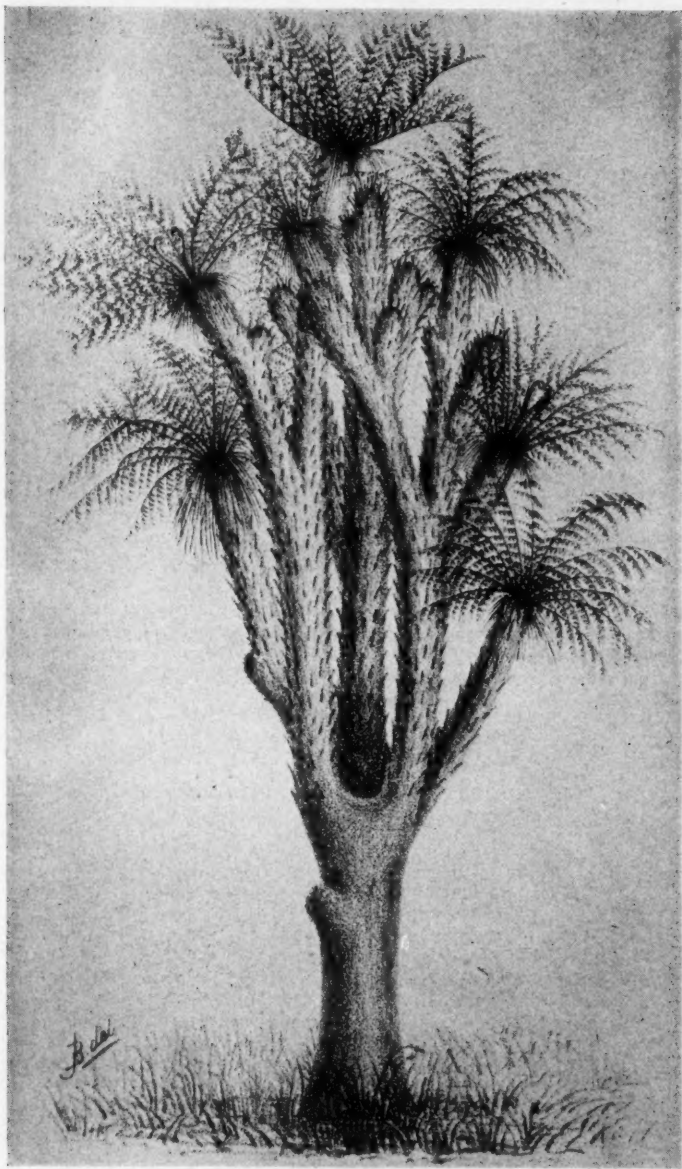
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## EXPLANATION OF PLATE

## PLATE 26

Fig. 30. A profusely branching specimen of the modern *Hemitelia Smithii* from New Zealand. From: Buchanan, J., On a remarkable branching specimen of *Hemitelia Smithii*. Trans and Proc. N. Z. Inst., pl. 12. 1886.



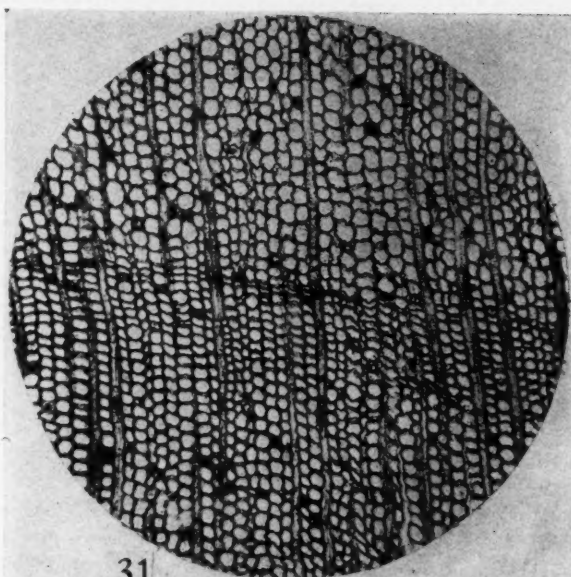
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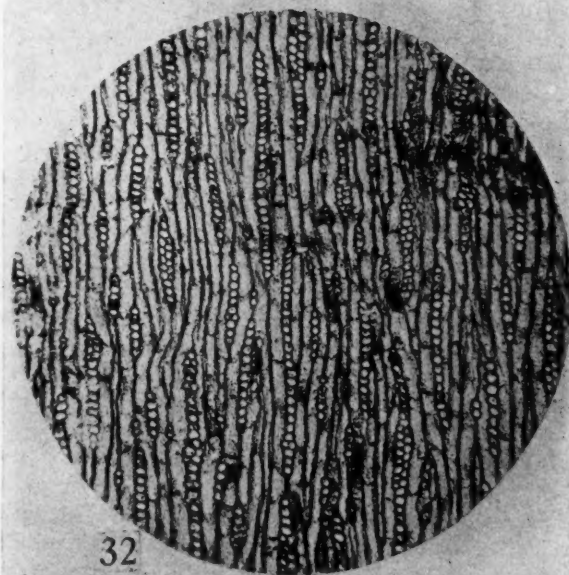
## EXPLANATION OF PLATE

## PLATE 27

Figs. 31, 32. Transverse and tangential sections respectively of a specimen of coniferous wood (*Cupressinoxylon* sp.) found associated with *Tempskya* east of Wayan, Idaho. Fig. 31 from slide No. 1474, specimen T8, x 62; fig. 32 from slide No. 1475, specimen T8, x 62.



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## APPENDIX

## SOME COMMENTS ON THE DISCOVERY OF TEMPSKYA IN THE VICINITY OF WAYAN, IDAHO

By C. HENRY THOMAS

In answer to your request I have included in the following lines a brief historical sketch of my *Tempskya*-collecting activities in the Wayan district.

I located in that part of the state in May, 1915, having migrated from the Scottsbluff country in Nebraska where I was raised on the frontier. Mine has been pretty much of an outdoor life. I was born in a one-room sod house in a still untamed country and have herded sheep or otherwise worked with livestock ever since the age of seven. As a boy I roughed and toughed it on the wind-swept prairies of western Nebraska, which were then treeless and monotonous with not even a shrub in sight. But since then they have been put under irrigation and become most productive and desirable.

After locating in the Grays Lake country of Caribou County I became occupied as a sheep herder and was naturally attracted to the odd and out-of-the-ordinary petrified fossil remains which are frequently seen on the range. At the time I did not know whether they were plant or bone, or in fact what they were; it was evident only that they were fossil remains. If bone it seemed most likely that they were saurians, or lizard-like reptile remains, and if plants, I had no idea of their origin.

Most of us are born with a sense of curiosity. We like to pry into the unknown. There are charms in new ventures, and thrills in first discoveries. Moreover, most of us are pack rats. We like to accumulate, although not many become enthralled with rocks.

I started gathering specimens in a small way almost simultaneously with my arrival on the Williamsburg bench. Later, as my collection had grown to a sizeable extent this matter became noised abroad, bringing a number of mineral collectors and rock-hounds from far and near. But no one knew what they were.

Myths and tales precede scientific knowledge. The human mind wants an explanation. And such settings gave birth to wild and fantastic tales. In one instance a certain oil-stock promoter, on visiting Mr. Sam Sibbett's ranch, claimed to be able to trace the outline of some huge bird which was of such gigantic proportions that it could seize an elephant by the nape of its neck! Such were the earlier local concepts of these interesting fossils that we later learned were petrified Tree fern trunks.

In the fall of 1936 I read in the Pathfinder of Mr. Roland W. Brown being associated with the Smithsonian Institution and doing paleontological work in Idaho and other far western states, so I sent some specimens to him for identification. Mr. Brown informed me that they were the so-called *Tempskyas*, or the petrified remains of a peculiar fern of the Cretaceous period.

Mr. Brown contacted Mr. W. W. Rubey (also of the U. S. Geological Survey) and as a consequence Mr. Rubey, who was doing field work on the Wyoming side

during the summer of 1937, came over to investigate. He expressed surprise at the abundance of Tempskyas in this region, and also took a number of leaf imprints of semi-tropical plants found in sedimentary rocks adjacent to grounds where Tempskyas weather out.

In August, 1938, Mr. Brown and Mr. Carl Mumm came to study the Tempskyas and the stratification of the beds out of which they weather.

Mr. W. A. Peters of Jerome, Idaho, who, of all rock-hounds, undoubtedly has the largest and most diversified collection in the state of Idaho, paid a visit in the spring of 1942 and brought with him Mr. Henry N. Andrews of the Missouri Botanical Garden, St. Louis. Mr. Andrews came at a favorable time of the year, when the snow was gone and there wasn't much vegetation to hide rocks, and the ground was soft so that they could readily be pried out with a wrecking bar. Paleobotanists know best how to appreciate plant remains of past geological ages. All those who have visited here have appeared to be highly interested and have commented on the excellent state of preservation of our Tempskyas.

During the summer of 1943 I herded sheep for Mr. Emil Stoor on ground adjoining my former holdings to the north and east, and that is when I really found most of my larger and better specimens.

This is an ever-changing world. Fossils are the evidence of the existence of former forms of plant and animal life. Scientists by tracing these clues endeavor to read the history of the earth's past geological transformations. Nothing just happens. Everything is the result of preceding forces. A rock is the product of nature's workings in the past.

